UNIVERSIDADE FEDERAL DO PARANÁ

MARCELO SOETH

ESTRUTURA POPULACIONAL, PADRÕES MIGRATÓRIOS E CONECTIVIDADE DE *Chaetodipterus faber* NO OCEANO ATLÂNTICO SUL

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Tese apresentada ao Programa de Pós-graduação em Sistemas Costeiros e Oceânicos, Centro de Estudos do Mar, Setor de Ciências da Terra, Universidade Federal do Paraná, como pré-requisito à obtenção do grau de Doutor em Sistemas Costeiros e Oceânicos.

Orientadores: Prof. Dr. Alberto Teodorico Correia
Prof. Dr. Henry Louis Spach
Prof. Dr. Felippe Alexandre Daros

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PREFÁCIO

A pesca desempenha um papel fundamental no fornecimento de alimentos, renda e emprego em muitas partes do mundo. Contudo, após intensa atividade pesqueira nas últimas décadas, muitas populações marinhas explotadas comercialmente apresentaram um declínio expressivo. Este cenário global tem redirecionado parte do esforço das frotas pesqueiras para outras espécies de menor valor comercial. Claramente, a sustentabilidade do setor pesqueiro e a conservação das populações explotadas e seus habitats depende da implementação de medidas eficazes de gestão pesqueira. Para isto, são necessários objetivos claros e um processo de tomada de decisão apoiado nas melhores informações disponíveis. Informações sobre recursos pesqueiros emergentes são escassas e usualmente não há medidas de manejo pesqueiro vigente para estas espécies. Na presente tese, sintetizamos informações de quatro anos de pesquisas sobre o paru, *Chaetodipterus faber*, usando ferramentas biológico-pesqueiras. O presente documento foi elaborado seguindo as normas do Programa de Pós-Graduação em Sistemas Costeiros e Oceânicos da Universidade Federal do Paraná. No primeiro capítulo, é apresentado uma introdução geral sobre a espécie em questão, a temática de pesquisa e os principais objetivos da tese. No segundo capítulo, foram avaliadas características da história de vida do paru aos 25 °S de latitude (Estado do Paraná) no Oceano Atlântico ocidental, incluindo idade, crescimento e reprodução. O terceiro capítulo teve o objetivo de delinear o estoque pesqueiro do paru na principal região pesqueira da espécie no Atlântico ocidental (entre o Estado do Espírito Santo e Santa Catarina), usando uma abordagem baseada nas características de forma e química dos otólitos. O quarto capítulo, teve o objetivo de avaliar nesta mesma região, o uso de áreas estuarinas nas fases iniciais de vida da espécie e os padrões migratórios em diferentes massas da água ao longo do seu ciclo de vida. E por fim, no quinto capítulo da tese, apresentamos as principais considerações sobre os nossos resultados para o direcionamento do manejo pesqueiro e conservação da espécie.

RESUMO

Na presente tese foram investigas características da história de vida do paru, *Chaetodipterus faber*, no Sul do Brasil e a estrutura do estoque pesqueiro nas principais áreas de pesca da espécie no Oceano Atlântico Sudoeste. Os resultados mais importantes desta tese foram: (1) próximo ao seu limite sul de distribuição *C. faber* tem uma longevidade de 17 anos; (2) o dimorfismo sexual no crescimento não foi evidente e a razão sexual (machos: fêmeas) foi de 1: 1,17; (3) a espécie apresenta crescimento assintótico que se ajusta a função crescimento de von Bertalanffy, onde os parâmetros estimados para todos os indivíduos coletados aos 25°S (Estado do Paraná) foram: L_∞ = 508,81 mm, k = 0,22 ano^{-1} e t_0 = -0,05 ano; (5) a espécie apresenta uma estratégia de desova parcelada com pico reprodutivo entre outubro e janeiro em latitudes subtropicais (25°S); (6) regiões estuarinas são importantes para a reprodução da espécie que, aparentemente, forma agregações reprodutivas nestas áreas; (7) as fêmeas gastam aproximadamente seis meses a mais que os machos para atingir a maturidade e são capazes de desovar pouco antes do seu segundo aniversário; (8) a forma e a química dos otólitos revelaram que a conectividade entre a população de *C. faber* na região do Espírito Santo (20°S) com as populações do sul (> 22°S) é limitada; (9) a presença de grupos semi-discretos espacialmente estruturados foi evidente entre 23°S e 27°S (Rio de Janeiro e Santa Catarina); (10) as razões de Sr/Ca e Mn/Ca ao longo dos marcos cronológicos nos otólitos de *C. faber* indica que a maioria dos indivíduos usa as regiões estuarinas na fase juvenil e migra para águas costeiras de maiores salinidades na fase adulta. Para fins de manejo pesqueiro, os nossos resultados sugerem que o defeso durante o pico reprodutivo e a proibição das capturas de indivíduos menores que 25 cm de comprimento total podem ser usados para a gestão do estoque de *C. faber* no Sul do Brasil; As unidades populacionais de *C. faber* na costa Sudeste e Sul do Brasil devem ser consideradas como diferentes estoques para fins de gestão pesqueira. No entanto, o grau de mistura e a contribuição que cada unidade populacional identificada recebe de fontes distantes de recrutamento são desconhecidas e exigem estudos adicionais. Por fim, os resultados reforçam a importância da conservação dos sistemas estuarinos que contribuem expressivamente para a manutenção das populações de *C. faber* no Oceano Atlântico Sudoeste.

Palavras-chave: Ephippidae · Crescimento · Reprodução · Microquímica de otólito · Análise de forma dos otólitos · Delineamento do estoque · Migração · Oceano Atlântico Sul

ABSTRACT

In this doctoral thesis some life-history traits of Atlantic spadefish, *Chaetodipterus faber*, in southern Brazil and the stock structure in the main fishery areas of the species in the Southwest Atlantic Ocean were investigated. The most important findings of this thesis were: (1) *C. faber* has a 17-year longevity close to its southern distributional limit; (2) sexual growth dimorphism was not evident and the male:female sex ratio was 1:1.17; (3) the species displayed asymptotic growth. Fitted von Bertalanffy growth function estimates for all individuals collected at 25°S (Paraná State) were L_{∞}= 508.81 mm, k= 0.22 year^{-1}, and t_0= -0.05 year; (4) the species is a batch spawner with a main reproduction period from October to January in subtropical latitudes at 25°S; (5) estuarine areas are important for *C. faber* reproduction that most likely exhibits a seasonal movement for spawning aggregation purposes; (6) females mature approximately 6 months later than males and are capable of spawning just prior to two years old; (7) the otolith shape and chemistry signatures indicated that connectivity between the population of *C. faber* in the Espírito Santo region (20°S) with the southern populations (>22°S) is limited; (9) the presence of spatially structured semi-discrete groups between 23°S and 27°S (Rio de Janeiro and Santa Catarina states) was evidenced; (8) the Sr/Ca and Mn/Ca ratios along chronological landmarks within the *C. faber* otoliths indicated that most individuals use the estuarine regions in the juvenile stage and thereafter migrate as adults to the open sea. To management proposes, the hereby results suggest that fishery closures during the spawning season and fishing size restrictions should be used to manage the *C. faber* stock in southern Brazil; The population-units should be regarded as different stocks for fisheries management purposes. However, at present, the degree of intermixing and the contribution that each local population identified receives from distant recruitment sources is unknown and demands further studies. Moreover, the current data reinforce the importance of estuarine systems conservation that plays a significant contribution as a nursery area for *C. faber* in southeastern-south Brazil.

Key-words: Ephippidae · Growth modeling · Reproduction · Otolith microchemistry · Otolith shape analysis · Stock delineation · Migration · South Atlantic Ocean

SUMÁRIO

CAPÍTULO 1

Introdução geral

INTRODUÇÃO GERAL

A espécie *Chaetodipterus Faber*

A família Ephippidae é composta por 8 gêneros e 15 espécies, das quais três compõem o gênero *Chaetodipterus* (Nelson, 2006; Eschmeyer e Fong 2018). O paru, *Chaetodipterus faber* (Fig. 1), é o único membro da família encontrado no Oceano Atlântico ocidental, integrando a cadeia trófica de águas costeiras desde Massachusetts (EUA) até o estado de Santa Catarina (Brasil), passando pelo Golfo do México e Mar do Caribe (Johnson, 1978; Burgess, 2002; Soeth et al., 2014; Machado et al., 2017). A espécie é considerada onívora, apresenta alta plasticidade trófica em todo seu ciclo de vida, podendo alimentar-se de algas, da epifauna bentônica de substrato consolidado e até de ovos de peixes no ambiente pelágico (Hayse, 1990; Barros et al., 2013). Alimenta-se de uma ampla faixa de cnidários bentônicos e planctônicos, entre hidrozoários, antozoários e cifozoários (Hayse, 1990), o que confere uma importante função ecossistêmica à espécie no controle deste grupo, que tem tendência a proliferar-se com o aumento das temperaturas dos oceanos devido às alterações climáticas (Brodeur et al., 2008). Além disso, Bellwood et al. (2006) consideram *C. faber* um candidato promissor para remoção efetiva de macroalgas em áreas onde estas tenham dominado a cobertura coralínea no Oceano Atlântico ocidental, como verificado pelos autores para *Platax pinnatus* (Ephippidae) no Oceano Pacífico ocidental. A espécie é também um importante item alimentar para predadores marinhos vulneráveis e ameaçados (IUCN), como *Epinephelus itajara* (Bullock e Smith, 1991; Gerhardinger et al., 2006), *Galeocerdo cuvier* (Bornatowski et al., 2007) e *Tursiops truncatus* (Gurjão et al., 2004), sendo assim um importante elo na passagem de energia entre os níveis tróficos. E ainda, por meio da exuberância dos seus grandes cardumes o paru, gera benefícios locais diretos para operadoras de mergulho recreativo (Comunicação pessoal, Operadora Maragogi Dive Sub).

Informações biológicas e ecológicas para *Chaetodipterus faber* e a família Ephippidae são ainda limitadas na literatura. *Chaetodipterus faber* pode alcançar mais de 6,5 kg em massa total (IGFA, 2017) e oito anos de idade (Hayse, 1990). Em regiões subtropicais do Oceano Atlântico Norte, machos e fêmeas de *C. faber* exibem uma maturação por volta de um ano de idade (Hayse, 1990). A espécie realiza desovas pelágicas (Chapman, 1978; Ditty et al., 1994) e aparentemente forma agregações reprodutivas, como evidenciado por observações visuais subaquáticas (Chapman, 1978; Heyman e Kjerve, 2008). Ovos e larvas da espécie têm sido

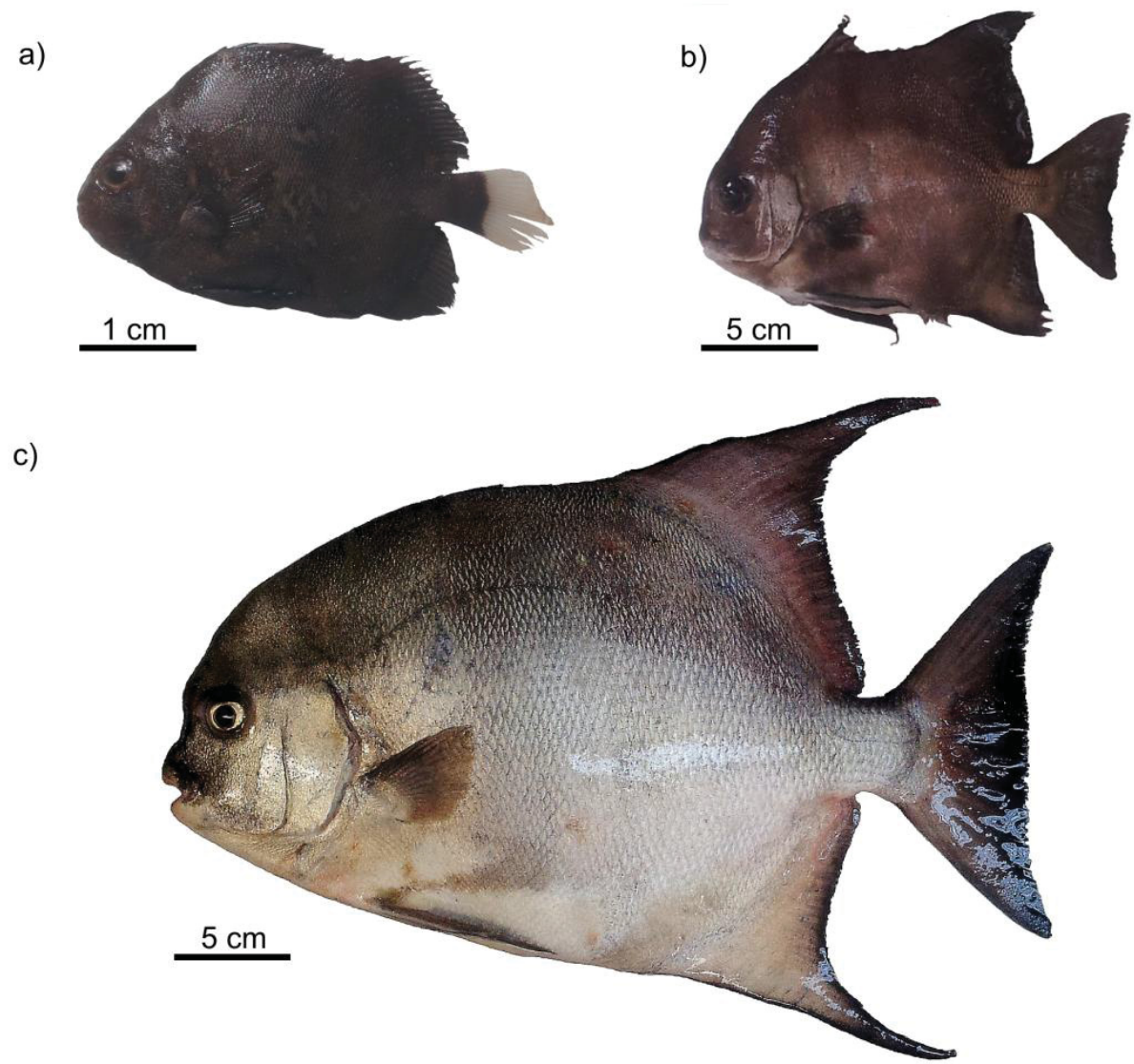

Figura 1. *Chaetodipterus faber* em diferentes fases ontogenéticas sendo (a) juvenil mimético e (b, c) adultos.

majoritariamente coletados durante a primavera e verão em canais de entrada ou no interior de baias e estuários (Barletta-Bergan et al., 2002; Joyeux et al., 2004; Castro et al., 2005; Bonecker et al., 2009; Burghart et al., 2014), ou em zonas costeiras e frentes estuarinas com salinidades entre 26 e 31 (Ditty et al., 1994). No norte do Golfo do México, a transição entre o período larval para a fase juvenil da espécie ocorre após 25 dias quando os indivíduos alcançam mais de oito milímetros de comprimento padrão, em temperaturas e salinidades médias de 28,7°C e 28,4, respectivamente (Ditty et al., 1994). *Chaetodipterus faber* é uma espécie eurihalina e tolera salinidades entre 15 e 37 (Sennett et al., 2011). Juvenis da espécie são capturados em amostragens direcionadas a ictiofauna demersal estuarina (Schwarz Jr. et al., 2007; Barletta et al., 2008), sendo ainda encontrados associados às raízes de árvores de

mangue (Osório et al., 2011), em ambientes praiais de baías (Pereira et al., 2014), praias estuarinas e planícies de maré (Santos et al., 2002; Hackradt et al., 2011; Vilar et al., 2011). Juvenis da espécie também ocorrem na plataforma continental interna, porém em números muito menores (na ordem de centena de vezes) que àqueles registros dentro dos estuários (Nakayama, 2004; Schwarz, 2008; Contente, 2013; Possatto et al., 2016). No complexo estuarino-lagunar de Cananéia-Iguape, Sudeste do Brasil, indivíduos entre 12 e 23 cm de comprimento total (1 a 2 anos de idade), são capturados durante todas as estações do ano (Hayse, 1990; Mendonça e Katsuragawa, 2001), indicando que a espécie pode permanecer por até dois anos em regiões estuarinas e migrar posteriormente para áreas costeiras de mar aberto. Na fase adulta, a espécie assume o comportamento bentopelágico, ocorrendo principalmente na coluna da água próximo a recifes rochosos, coralíneos e artificiais localizados na plataforma continental interna (Hayse, 1990; Bizerril e Costa, 2001; Godoy et al., 2002; Luiz Jr. et al., 2008; Hackradt e Félix-Hackradt, 2009).

Nas últimas décadas, além dos impactos indiretos da perda de importantes habitats para juvenis de peixes, como as florestas de mangue (Valiela et al., 2001; Contente et al., 2011), a pesca excessiva sobre várias espécies marinhas, levaram a um decréscimo de muitas populações (Jackson et al., 2001; Myers e Worm, 2003; Begossi et al., 2017), conduzindo uma transição gradual nas pescarias em direção a populações de menores níveis tróficos (Pauly et al., 1998), fazendo com que espécies consideradas menos importantes para o consumo, como *C. faber*, passassem a ter a captura e o valor comercial incrementados (IBAMA, 2007; UNIVALI/CTTMar, 2013; PMAP-SC, 2018). Nos Estados Unidos, as pescarias recreativas de *C. faber* têm experimentado um desenvolvimento especializado e crescido em popularidade nas últimas décadas (Bell, 2005). No Brasil, além de ser uma espécie alvo de pescarias recreativas (Pinheiro et al., 2010), o paru é principalmente capturado pela frota artesanal e industrial que desembarcou uma média anual de 250 toneladas ao longo da costa brasileira na última década (IBAMA, 2007; MPA, 2012). *Chaetodipterus faber* faz agregações em áreas costeiras, principalmente durante a primavera e verão, facilitando ainda mais a captura dos indivíduos (Bell, 2005; PMAP-BS, 2017a, 2017b). Este período parece coincidir com o período reprodutivo (Hayse, 1990; Castro et al., 2005), o que aumenta o risco de sobreexplotação, como observado para outras espécies de importância comercial (Sadovy de Mitcheson et al., 2008; Sadovy de Mitcheson et al., 2013; Lemos et al., 2014; Van Overzee e Rijnsdorp, 2014; Chao et al., 2015). Adicionalmente, a frota industrial de cerco que atua na plataforma continental do Sudeste e do Sul do Brasil, tem empregado parte do seu esforço pesqueiro à captura deste recurso. A média anual de *C. faber* desembarcado no estado de

Santa Catarina passou de 36 toneladas entre os anos de 2000 e 2011 para mais de 240 toneladas entre 2012 e 2017 (UNIVALI/CTTMar, 2010, 2013a, 2013b; PMAP-SC, 2018). O desembarque da espécie pela frota de cerco também ocorre em Angra dos Reis (RJ) e a comercialização deste recurso se estende, pelo menos, até os estado do Espírito Santo e Bahia [comunicação pessoal com fornecedores locais de Guarapari (ES) e Salvador (BA)]. O comportamento de formar cardumes torna *C. faber* particularmente vulnerável à frota industrial de cerco, como observado para outras espécies como o arenque e sardinha (Misund, 1993; PMAP-SC, 2018). Apesar da participação relativa pequena do *C. faber* nos desembarques totais realizados pela frota industrial de cerco nesta região, às biomassas anuais desembarcadas de *C. faber* por esta frota na última década são maiores que àquelas realizadas pela frota artesanal (UNIVALI/CTTMar, 2010, 2013a, 2013b; PMAP-BS, 2017a, 2017b; PMAP-SC, 2018). Atualmente, a frota de cerco está autorizada a realizar o desembarque do paru (IN MPA/MMA n° 10 2011), porém não há legislação específica que direcione o manejo pesqueiro da espécie.

Estudos de idade, crescimento e reprodução

A urgência em se estudar e avaliar recursos pesqueiros emergentes, mas sem quaisquer informações de biologia pesqueira, é evidente. Nos ambientes marinhos, os efeitos da sobrepesca estão entre os protagonistas da perda de biodiversidade (Jackson et al., 2001; Meyer e Worm, 2003). A pesca é um agente de seleção artificial, causa mudanças fenotípicas e genéticas em populações pescadas de maneira que não apenas inibem a produtividade e a estabilidade das capturas, mas desestabilizam a dinâmica das populações de peixes, causando danos muitas vezes irreversíveis (Hixon et al., 2014).

As características da história de vida das espécies e populações de peixes são extremamente diversas (Pauly, 1980; Vazzoler, 1996); conhecer essas características, como por exemplo, o crescimento e a reprodução das populações explotadas é essencial para o sucesso do manejo pesqueiro e da conservação das populações e espécies (Harry et al., 2013; van Overzee e Rijnsdorp, 2014; Aschenbrenner et al., 2017). Informações sobre o tamanho de primeira maturação e do período reprodutivo podem ser usadas como referências biológicas para a tomada de decisões de manejo, como por exemplo, as restrições de captura por tamanho e época de desova (Yamahira, 2004; Lowerre-barbieri, 2009; van Overzee e Rijnsdorp, 2014). Além disso, dados de comprimento e idade dos indivíduos são essenciais

para verificar quais classes etárias são pescadas (Cergole et al., 2005; Vaz-dos-Santos, 2015), estimar parâmetros biológicos incluindo taxas de crescimento e mortalidade natural que são críticos para modelar a dinâmica populacional e a biomassa dos estoques pesqueiros (Pauly, 1980; He et al., 2016; Ogle, 2016; Aschenbrenner et al., 2017).

O estudo e interpretação da idade e do crescimento por meio de estruturas calcificadas é denominado Esclerocronologia (do grego, sklerós = duro e khronológia = ciência do tempo). Escamas, otólitos, ossos operculares, raios de nadadeiras e vértebras são exemplos de estruturas comumente usadas em inferências de idade e crescimento (Campana e Neilson, 1985). Otólitos são as estruturas mais frequentemente usadas visto que não sofrem reabsorção posteriormente a sua formação (Campana et al., 2000). Otólitos estão localizados no ouvido interno dos peixes teleósteos e estão relacionados à função de equilíbrio corporal e audição (Popper e Lu, 2000). Nestas estruturas calcificadas, formam-se zonas opacas e translúcidas, resultante de períodos com menor e maior deposição de carbonato de cálcio, matéria orgânica e de outros elementos que constituem os otólitos (Morales-Nin, 2000). O acréscimo de cálcio e microelementos é um processo extracelular, regulado por hormônios e fatores exógenos (Morales-Nin, 1986; Pannella, 1980; Beckman e Wilson, 1995), os quais se podem destacar, os ciclos diários de luz (foto-período) (Wright et al., 1992) e os ciclos sazonais de temperatura, chuva e disponibilidade de alimento (Campana, 1984; Ralston, 1995). Diversos estudos têm examinado a relação destes e outros fatores ambientais, cíclicos e não cíclicos, no incremento e formação dos otólitos (Panfili et al., 2002). Contudo a temperatura destaca-se como fator preponderante (Casselman, 1990). Em resumo, as variações exógenas e endógenas alteram a as taxas de deposição nos otólitos, resultando na formação de zonas mais e menos calcificadas (Secor et al., 1991).

A presença de incrementos diários discerníveis em otólitos de larvas e juvenis é uma característica que fornece precisão na estimativa de idade de peixes (Campana e Neilson, 1985). Estas informações têm sido usadas para determinar taxas de crescimento durante as fases iniciais de vida e estimar o tempo do período larval de peixes (Campana, 2001). Além disso, a variação ontogenética na morfologia dos otólitos pode ser relacionada a uma transição na fisiologia, habitat ou comportamento (Panfili et al., 2002). Na maioria das espécies de peixes a metamorfose é a transição que marca o final do período larval. Neste período, a formação de centros acessórios de crescimento pode ser registrada nos otólitos, como visto nos pleuronectiformes (Campana e Neilson, 1985; Fischer, 1999; Neuman et al., 2001; Panfili et al., 2002). Não distante, no fim do período larval também ocorre o fim da respiração

cutânea e a ossificação completa (Panfili et al., 2002), a troca de íons com o ambiente é limitada pelo transporte via brânquias e trato digestivo (Campana, 2001).

Quando é comprovada a periodicidade da formação dos anéis, cada grupo de anel passa a caracterizar uma classe etária ou coorte (Sparre e Venema, 1992). As informações validadas, juntamente com as informações de peso e comprimento, são então passíveis de uso em modelos analíticos para estimar os parâmetros de crescimento corpóreo, como os parâmetros da curva de crescimento de von Bertalanffy que considera a idade como a variável independente (x) e o comprimento ou peso corporal na idade a variável resposta (y) (Vaz-dos-Santos, 2015). A função de crescimento de von Bertalanffy (VBGF), é a equação mais utilizada para modelar o crescimento de peixes, baseia-se no pressuposto de que a alteração corporal ao longo do tempo resulta da diferença entre o processo de construção somática (anabolismo) e de degeneração de tecido (catabolismo) (Minte-Vera et al., 2016). Contudo, em muitos casos, a VBGF não é a mais adequada, e para muitas outras espécies aquáticas, outros modelos de crescimento, como o modelo Gompertz (Gompertz, 1825) ou o modelo logístico (Ricker, 1975) descrevem melhor o crescimento individual (Katsanevakis e Maravelias, 2008). Testar múltiplos modelos de crescimento individual aos dados de comprimento-idade e usar um critério adequado de seleção dos modelos pode reduzir o potencial de erro, inerente à escolha com base no ajuste visual do modelo ao conjunto de dado (Akaike, 1981; Burnham e Anderson, 2002; Katsanevakis, 2006; Corey et al., 2017).

As estratégias reprodutivas nos teleósteos marinhos são extremamente diversas e incluem espécies semélparas com desova total (ex., salmão do alasca) e parcelada (ex., enguia-europeia), espécies iteróparas com desova total (ex., arenque do atlântico) e parcela, podendo a última apresentar desenvolvimento sincrônico (ex., tainha) ou desenvolvimento assíncrono (ex., maria-luísa) (Costa et al., 2015; Lemos et al., 2014; Lowerre-Barbieri et al., 2011). Apesar da diversidade de estratégias reprodutivas, os traços compartilhados pelas espécies de peixes têm permitido a padronização da terminologia para a descrição e classificação do desenvolvimento reprodutivo e gonadal de peixes, essencial para estudos comparativos (Brown-Peterson et al., 2011). As avaliações do desenvolvimento gonadal permitem identificar, por exemplo, períodos reprodutivos, realizar estimativas de fecundidade e de tamanho de primeira maturação em populações de peixes (Costa et al., 2015; Hayse, 1990; Lemos et al., 2014; Lowerre-Barbieri et al., 2011). A classificação dos estágios de desenvolvimento gonadal tem se baseado em critérios macroscópicos, incluindo aparência externa da gônada e índice gonadossomático, e critérios microscópicos, incluindo aparência do ovócito inteiro e técnicas mais apuradas de histologia (West 1990; Dias et al., 1998;

Fontoura et al., 2018). A classificação baseada em técnicas histológicas representa o método mais preciso e produz a maior quantidade de informação, incluindo aspectos detalhados da gametogênese, essenciais para avaliar a dinâmica reprodutiva (Dias et al., 1998; Costa et al., 2015, Bueno et a., 2016).

Conectividade e estrutura populacional

A conectividade populacional é a troca de indivíduos entre subpopulações geograficamente separadas que compõem uma metapopulação (i.e., um conjunto discreto de populações locais com alguma migração mensurável compartilhada entre elas) (Cowen e Sponaugle, 2009). O conceito de metapopulação pode ser ainda mais detalhado, sendo descrito como um sistema de populações locais discretas, cada qual determina, em grande parte, a sua própria dinâmica interna, mas com um grau de influência demográfica identificável e não trivial de outras populações locais por meio da dispersão dos indivíduos (Kritzer e Sale, 2004). Peixes recifais comumente residem em um complexo mosaico costeiro onde a dinâmica populacional é inerentemente relacionada à conectividade ocorrendo sobre muitas escalas de tempo (ecológico e evolucionário) e espaço (habitats, ecossistemas e oceanos) (Mumby e Hastings, 2008; Correia et al., 2012; Rooker et al., 2018). O nível de tal conectividade determina, por exemplo, a extensão nos quais os processos demográficos de imigração e emigração contribuem para a regulação e reabastecimento de populações em outras áreas (Hamer et al., 2011; Mensink e Shima, 2016; Fowler et al., 2017).

A definição de população é semelhante à definição de estoque pesqueiro, entretanto, o estoque refere-se, essencialmente, a recursos explotados comercialmente e que integram as estratégias de gestão pesqueira (Begg e Waldman, 1999). Numerosos conceitos de estoques podem ser encontrados na literatura da ciência pesqueira. Uma definição amplamente aceita para estoque pesqueiro é, um grupo semi-discreto intraespecífico de uma unidade populacional com características homogêneas no espaço-tempo (Ihssen et al., 1981). É componente fundamental da gestão, pois define as unidades básicas de trabalho sobre o qual o recurso é avaliado, visando à explotação sustentável (Begg et al., 1999; Tanner et al., 2016). A estrutura da população e do estoque podem ser inferidas por diversas técnicas, baseada na maioria das vezes nas variações fenotípicas e genotípicas (Begg et al., 1999) (Figura 2). O fenótipo (aparência, estrutura, fisiologia e comportamento) de qualquer organismo é determinado pela interação entre o ambiente com seu genótipo, que é o produto final de muitos mecanismos que promovem a diversidade genética entre populações (Hirsch, 1963). A

plasticidade fenotípica é a capacidade de um único genótipo em exibir fenótipos variáveis em diferentes ambientes (Whitman and Agrawal, 2009). Ou seja, fatores ambientais podem afetar e alterar a expressão dos genes, enquanto os genes podem definir como os organismos responderão a diferentes ambientes (Lobo e Shaw, 2008).

Abordagens fenotípicas são muitas vezes vantajosas, comparativamente aos estudos clássicos de genética molecular, nomeadamente com recurso ao DNA mitocondrial (mtDNA), uma vez que as espécies marinhas costeiras por via de uma fase larval longa e elevada dispersão dos indivíduos, muitas vezes não têm padrões genéticos de diferenciação espacial, consequência do elevado fluxo gênico associado a estas espécies (Correia et al., 2012). Ainda assim, embora muitas questões de identificação de estoques pesqueiros possam ser respondidas com dados de conectividade genética, métodos genéticos sozinhos produzem pouca informação em relação à conectividade demográfica, que definimos como o grau em que o crescimento da população e as taxas vitais são afetados pela dispersão dos indivíduos (Lowe e Allendorf, 2010).

A diferenciação populacional é determinada por processos evolutivos (ex., seleção natural, fluxo gênico, deriva genética e mutação) e contemporâneos, incluindo dispersão larval, barreiras oceanográficas e dinâmica populacional (Chakraborty e Leimar, 1987; Selkoe et al., 2008; Lowe e Allendorf, 2010). Barreiras físicas podem modelar diferenças populacionais resultando assim em variação genética entre populações (Lowe e Allendorf, 2010). Níveis reduzidos de fluxo gênico e diferenças ecológicas entre habitats podem conduzir a uma adaptação local e promover especiação em longo prazo (Barton e Hewitt, 1985). Porém, quando o fluxo gênico ocorre entre populações, mesmo em baixas quantidades, as frequências alélicas podem tornar-se homogêneas (Slatkin, 1985). Neste sentido, a conectividade genética pode ser definida como o grau no qual o fluxo gênico afeta processos evolutivos dentro de subpopulações (Lowe e Allendorf, 2010). Ao contrário da conectividade genética, a qual é principalmente uma função do número absoluto de dispersores, a conectividade demográfica é uma função da contribuição relativa da imigração líquida (isto é, imigração - emigração) ao recrutamento total numa população. O recrutamento total é o número de "novos" indivíduos no tempo t + 1, que não estavam presentes no momento t, ou seja, $N_{t+1} = N_t$ +Nascimentos - Mortes (i.e., recrutamento local) + Imigrantes - Emigrantes (i.e., rede de migração) (Lowe e Allendorf, 2010). A resposta para esta equação não é simples e na maioria das vezes requer o uso de marcadores artificiais. Entretanto, mesmo as tecnologias mais desenvolvidas ainda não são aplicáveis para todos os organismos, dado a diversidade de comportamento e o tamanho dos mesmos (Begg e Waldman, 1999; Tanner et al., 2016). Neste

sentido, o uso de abordagens holísticas, combinado técnicas fenotípicas e genotípicas tem sido sugerida (Correia et al., 2012; Tanner et al., 2014).

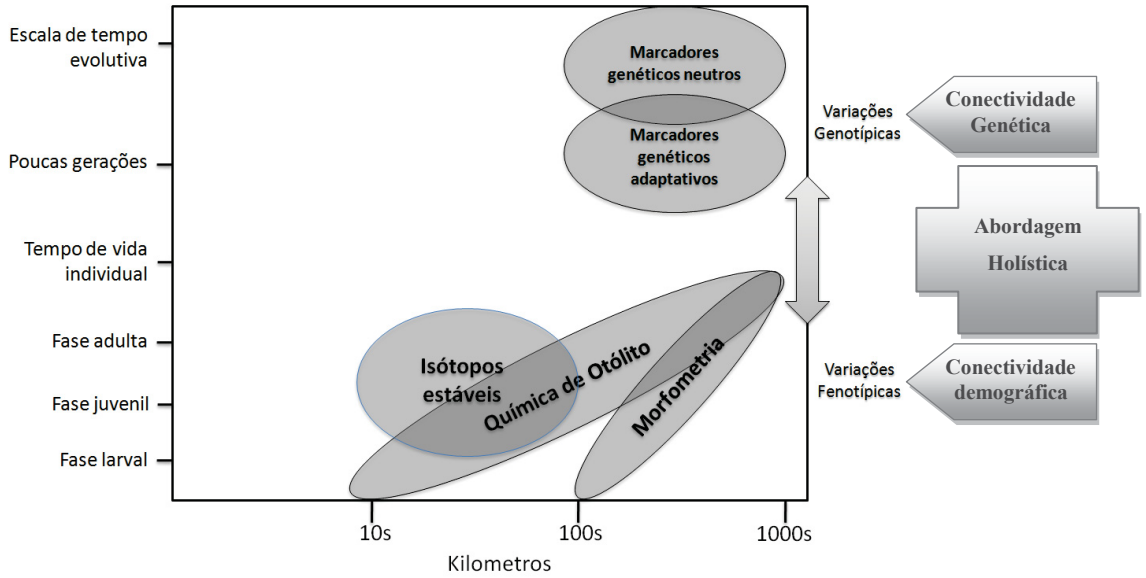

Figura 2. Diferentes escopos espaços-temporais das distintas técnicas baseada nas variações fenotípicas e genotípicas aplicadas na identificação de estoques pesqueiros. Adaptado de Tanner et al. (2016).

Em uma pequena escala evolutiva de aproximadamente 10 milhões de anos, a ictiofauna marinha do Oceano Atlântico Ocidental tem sido moldada pelo estabelecimento da descarga fluvial dos rios Amazonas e Orinoco, que "filtrou" efetivamente a fauna costeira de água rasa do Caribe da brasileira (Rocha, 2003; Floeter et al., 2008), e pelo fechamento do Istimo do Panamá (Coates e Obando, 1996), que além de separar a fauna ocasionou mudanças oceanográficas (O'Dea et al., 2007; Rocha et al., 2008). No que se refere à primeira barreira, não há evidências ou estudos que mostrem a efetividade da mesma em governar eventos de especiação em *Chaetodipterus* (Machado et al., 2017). Entretanto, a barreira sólida do Istimo do Panamá originou *Chaetodipterus zonatus* (Girard, 1858), o qual se distribui pelo leste da costa do Pacífico, entre a Califórnia (USA) e o Peru (Froese e Pauly, 2015). Da mesma forma, a barreira formada pelos mais de 3500 km de águas profundas e oligotróficas do Atlântico (Floeter et al., 2008), entre a zona costeira da África e da América do Sul, formada a 84 milhões de anos atrás (Pittman et al., 1993), manteve *Chaetodipterus lippei* (Steindachner, 1985) distante das águas brasileiras.

Ao longo da costa brasileira *C. faber* possui uma estruturação genética ao nível de mtDNA entre a região tropical (<20°S) e subtropical (>23°S), com indicativos de divergência

alopátrica da população subtropical (Rio de Janeiro a Santa Catarina) a qual apresenta baixa diversidade genética (Machado et al., 2017). Dentro das duas grandes regiões definidas (Tropical e Subtropical), fluxos gênicos em baixas quantidades poderiam tornar as frequências alélicas homogêneas (Slatkin, 1985). Desta forma, outras abordagens poderiam ser empregadas para complementar aspectos referentes à conectividade demográfica e oferecer uma visão holística e de suporte as definições das unidades populacionais e/ou estoques explotados.

Ao longo da costa brasileira, a conectividade de *C. faber* provavelmente ocorre em dois principais pulsos durante o seu ciclo de vida, de forma passiva e ativa. Muitos organismos marinhos, como *C. faber*, possuem larvas pelágicas que podem interligar populações distantes através da dispersão passiva destes estágios nas correntes oceânicas (Taylor e Hellberg, 2003). Com desova e fase larval pelágica (Ditty et al., 1994), larvas planctônicas de *C. faber* podem derivar passivamente por dezenas a centenas quilômetros do local de postura dos ovos até os locais de desenvolvimento dos juvenis, quando consideramos uma corrente com velocidade média entre 0,28 a 0,56 km/hora sobre a plataforma continental brasileira (Silveira et al., 2000; Zavialov et al., 2002). Espécies com tais características devem apresentar-se geneticamente homogêneas sob largas escalas espaciais (Siegel et al., 2008). No entanto, a história de vida e a circulação costeira caótica regulam a natureza estocástica da dispersão larval, o que torna pouco preciso os modelos físicos disponíveis (Ditty et al., 1994; Siegel et al., 2008; Burghart et al., 2014; Machado et al., 2017). Evidências apresentadas pela literatura de que a espécie realiza a desova em áreas de influência estuarina (Ditty et al., 1994; Castro et al., 2005), poderia ser uma tática na qual a consequência para espécie aumentaria a retenção larval e beneficiaria os juvenis demersais por meio do seu assentamento em áreas favoráveis ao desenvolvimento, isto é, ambientes estuarinos. Ainda neste sentido, há evidências que a espécie sincroniza sua desova com as oscilações de maré (lua) (Heyman e Kjerve, 2008), o que poderia ocasionar a diminuição da dispersão da prole, como verificado para outras espécies de teleósteos marinhos (Erisman et al., 2012; Thorrold et al., 2001). Assim, os complexos mecanismos envolvidos na retenção das larvas em sua origem natal, proporcionariam uma grande oportunidade de estruturação populacional (Taylor e Hellberg, 2003). As variações fenotípicas ocasionadas neste curto e importante período larval podem ser acessadas via química dos otólitos, baseada na variabilidade geográfica da composição química dos otólitos (Tanner et al., 2014). Embora as diferenças fenotípicas não providenciem evidências de isolamento genético, eles podem indicar separação pós-larval prolongada, diferenciada pelos regimes ambientais (Campana et al., 1995). Desta forma, é esperado que as

diferentes áreas habitadas por *C. faber* ao longo do seu ciclo de vida sejam visualizadas como distintas assinaturas químicas nos otólitos (Thorrold et al., 2001), com aumento nestas diferenças entre regiões de maior heterogeneidade ambiental (Reis-Santos et al., 2013; Daros et al., 2016a)

Apesar de não contemplado por literatura especifica, *C. faber* apresenta uma clara mudança ontogenética em relação ao uso de habitat. Uma ampla diversidade de espécies de peixes recifais (ex., meros, sargos e caranhas) utilizam ambientes estuarinos durante sua fase juvenil de vida e migram posteriormente para ambientes recifais da plataforma continental (Aschenbrenner et al., 2016; Correia et al., 2011; Orian E. Tzadik et al., 2017). Esta mudança ontogenética no uso de habitat inclui a necessidade de diferentes recursos alimentares, vulnerabilidade a predadores, e a necessidade de se reproduzir em locais que ofereçam as maiores sobrevivências e desempenho de crescimento dos seus descendentes (Laegdsgaard e Johnson, 2001; Thorrold et al., 2001; Mumby e Hastings, 2008). Além disso, migrações diárias e sazonais evitam condições ecológicas e ambientais desfavoráveis e podem representar a única oportunidade de reprodução (Domeier e Colin, 1997; Mumby e Hastings, 2008; McKeown et al., 2015; Rooker et al., 2018). Como hipotetizado por Clark's (1968) e revisado por Secor (1999), a divergência na mudança de habitats (migração) dentro da população resultaria na manutenção de comportamentos "retentivos" e "exploratórios", o que contribuiria para a regulação populacional por meio de fatores que incluem persistência, contração-expansão e colonização (Figura 3), ou seja, a formação de diferentes contingentes intrapopulacionais. Padrões divergentes de migração podem ainda ser mais expressivos em espécies com desova parcelada devido à correspondência ou incompatibilidade entre as desovas (isto é, os nascimentos) e as condições ideais para o crescimento, como disponibilidade de alimento e temperaturas favoráveis (Olson, 1996; Secor, 1999; Lowerre-Barbieri et al., 1998, 2011b). Nas últimas décadas, uma crescente perspectiva sobre a prevalência e a importância ecológica de migrações divergentes dentro de populações expandiu a definição tradicional de estoque pesqueiro (Fowler et al., 2016; Mai et al., 2014; Secor, 1999). Grande parte da compreensão da presença de grupos migratórios intrapopulacionais divergentes (contingentes) só foi possível por meio do desenvolvimento de ferramentas analíticas sensíveis e capazes de acessar marcadores naturais informativos nos otólitos (ex., ^{7}Li, ^{25}Mg, ^{55}Mn, ^{65}Cu, ^{66}Zn, ^{88}Sr, ^{85}Rb, ^{138}Ba e ^{208}Pb) (Mai et al., 2014; Fowler et al., 2016; Tanner et al., 2016).

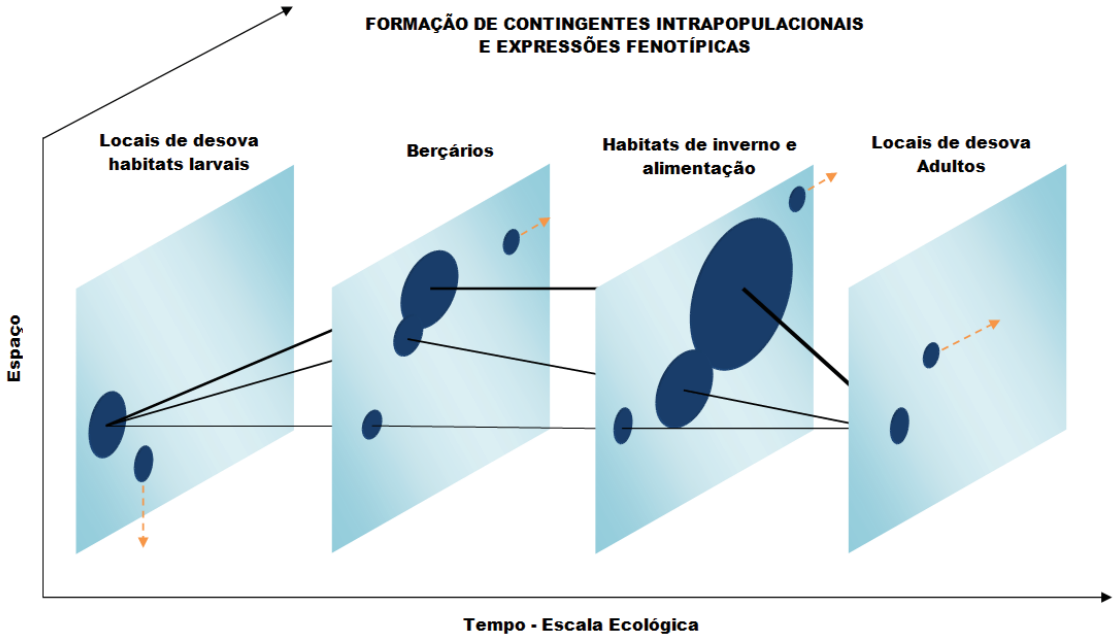

Figura 3. Possível cenário da trajetória migratória para três contingentes comportamentais intrapopulacionais. Cada painel representa um corte transversal no tempo da ocorrência espacial (longitude e latitude). Painéis estão dispostos da esquerda para direita (escala ecológica) para mostrar as mudanças ontogenéticas nos padrões de migração. Principal circuito migratório é apresentado pela linha em negrito. Tamanho dos centroides representa o nível de dispersão dos agregados populacionais. Flechas pontilhadas laranjas indicam supostas perdas por destinos migratórios errôneos. Adaptado de Secor (1999).

Microquímica de otólitos

Otólitos são estruturas calcificadas pareadas, metabolicamente inertes e com características intrínsecas amplamente utilizadas para estimar a idade de peixes ósseos (Campana, 1999; Popper e Lu, 2000; Correia et al., 2009). À medida que os otólitos dos peixes crescem, a deposição continua e concêntrica de camadas de carbonato de cálcio ($CaCO_3$) e elementos traços originam anéis de crescimento com periodicidade anual, sazonal e diária, registrando as informações da história de vida em uma sequencia cronológica (Campana, 1999). A incorporação dos elementos na matriz aragonítica dos otólitos a partir da água circundante e dos alimentos é um processo complexo que envolve o transporte de íons dissolvidos sobre várias membranas (Payan et al. 2004; Thomas et al. 2017) e não é necessariamente um reflexo direto da composição do ambiente circundante ou da dieta (Sturrock et al., 2015, 2014). Embora a incorporação dos diferentes elementos nos otólitos seja ainda um processo pouco compreendido, alguns elementos, como o estrôncio e o bário,

apresentam altas correlações entre a concentração ambiental e a otolítica (Albuquerque et al., 2010; Bath et al., 2000; Webb et al., 2012). Desta forma, devido ao seu crescimento contínuo e inércia metabólica, os otólitos têm sido marcadores naturais úteis no estudo de movimentos e migrações de peixes (Correia et al., 2004; Gillanders, 2005), diferenciação de estoques pesqueiros (Correia et al., 2011, 2014), determinação de locais de nascimento (Hamer et al., 2011) e em estudos de conectividade entre berçários e zonas de recrutamento costeiro (Reis-Santos et al., 2012; Correia et al., 2012). Um grande número de elementos químicos pode ser avaliado nos otólitos (Correia et al., 2012). Estrôncio (Sr) e Bário (Br) podem indicar, por exemplo, o movimento de peixes através de um gradiente salino (Campana, 1999). Enquanto as razões de Sr/Ca na água usualmente incrementam com o aumento de salinidade, as razões de Ba/Ca apresentam geralmente o padrão inverso (Bath et al., 2000; Elsdon et al., 2008; Albuquerque et al., 2010). Influências fisiológicas também são conhecidas sobre alguns elementos, incluindo o zinco (Zn). Devido à sua função durante a maturação ovariana, menores concentrações de Zn estão disponíveis no plasma sanguíneo de fêmeas adultas neste período, e consequentemente menores razões de Zn/Ca são observadas nas seções do otólito representando o período reprodutivo (Sturrock et al., 2014; Sturrock et al., 2015), sendo assim um possível e interessante marcador natural do ciclo reprodutivo. Efeitos maternos também ocorrem sobre a composição química do núcleo dos otólitos, nomeadamente sobre o manganês (Mn). Um aumento expressivo nas concentrações de Mn no ovo, associado ao desenvolvimento embriológico e ao material materno, podem produzir níveis elevados de Mn na porção do otólito que representa o estágio inicial de vida (ovo e larva) (Brophy et al., 2004; Ruttenberg et al., 2005).

Embora considerada uma ciência em desenvolvimento, a composição química dos otólitos têm se mostrado uma ferramenta poderosa na resolução da estrutura populacional de peixes caracterizados por um elevado fluxo gênico, sobretudo quando existe uma heterogeneidade ambiental que se reflete na composição química dos otólitos (Selkoe et al., 2008; Smith e Campana, 2010; Correia et al., 2012). Os otólitos têm-se revelado úteis no estudo do ciclo de vida de peixes, em alternativa aos métodos tradicionais de marcação e recaptura, sendo também uma ferramenta complementar a biologia molecular e estudos de parasitologia (Selkoe et al., 2008; Smith e Campana, 2010; Correia et al., 2012). O uso das assinaturas químicas dos otólitos para responder questões referentes à estrutura populacional e ciclo de vida requer um desenho experimental adequado, espécie-específica, e o respeito por um conjunto de premissas metodológicas (Eldson et al., 2008). Atualmente há diversos métodos analíticos disponíveis, com grande variação de custo e precisão analítica, os quais

acessam a informação química dos otólitos por dois métodos principais, a digestão ácida dos otólitos inteiros e a análise de secções dos otólitos (Avigliano e Volpedo, 2015).

A digestão do otólito inteiro tem sido emprega principalmente em estudos de discriminações de estoques pesqueiros. Este método transforma toda a informação temporal existente nos otólitos em um único valor médio para cada elemento analisado (Begg e Waldman, 1999). Sustenta-se na premissa que em um compartimento aquático heterogêneo diferentes propriedades físico-químicas do ambiente aquático irão produzir distintas assinaturas químicas (Thorrold et al., 1998). Neste sentido, para se evitar e minimizar o "ruído" temporal e ontogenético na variabilidade espacial das assinaturas químicas, como consequência de materiais recém-acrescidos nos otólitos que podem potencialmente confundir as assinaturas de grupos espaciais pré-estabelecidos (Tanner et al., 2016), algumas premissas metodológicas devem ser observadas destacando-se a amostragem dos indivíduos em pequenas janelas temporais (menor que seis meses) e a seleção de grupos de idade (coortes) (Gillanders e Kingsford, 2000; Rooker et al., 2001; Eldson et al., 2008; Daros et al., 2016a, 2016b). Os limites de detecção dos equipamentos para cada elemento químico também é essencial na escolha dos diversos métodos disponíveis para a análise química dos otólitos digeridos (Kraus e Secor, 2004; Avigliano e Volpedo, 2015). Para a análise dos otólitos digeridos registra-se o uso de espectrometria de absorção atômica (AAS) (Grady et al., 1989; Hanson et al., 2004), espectroscopia de emissão atômica através de plasma indutivamente acoplado (ICP-AES) (Miyan et al., 2016), espectrometria de emissão atômica por plasma acoplado indutivamente (ICP-OES) (Avigliano et al., 2017) e espectrometria de massas através de plasma indutivamente acoplado (ICP-MS) (Correia et al., 2012).

A análise de determinadas porções dos otólitos correspondentes a períodos específicos de vida conduz a avaliações espaços-temporais de alta resolução (Tanner et al., 2016). Pode ser usada em paralelo à definição da existência de uma estrutura metapopulacional, oferecendo uma perspectiva potencialmente esclarecedora sobre o desempenho de cada fase da vida na conectividade da metapopulação (Sih e Kingsford, 2016; Pita et al., 2016). Além disso, analisando secções do otólito é possível rastrear a história de vida passada dos indivíduos, determinar locais de nascimento, verificar a conectividade entre berçários e zonas de recrutamento costeiro (Hamer et al., 2011; Reis-Santos et al., 2012; Correia et al., 2012). As técnicas analíticas geralmente empregadas para análise de otólitos seccionados são microssonda eletrônica (EPMA) (Daros et al., 2016b), emissão de raios X induzida por micropartículas (Micro-PIXE) (Zhong et al. 2007; Jiang et al., 2012) e ablação a laser acoplado a espectrometria de massas por plasma indutivamente (LA-ICP-MS). O

acoplamento de ablação a laser ao ICP-MS é considerado um marco na análise química de otólitos (Tanner et al., 2016). Em função da sua sensibilidade analítica, é provavelmente a técnica mais utilizada nos últimos anos (Avigliano e Volpedo, 2015).

Morfometria de otólitos

Os três pares otolíticos (sagittae, lapilli e asterisci) estão presentes em todos os peixes Teleostei e apresentam características específicas, que possibilitam a identificação de espécies (Rossi-Wongtschowski et al., 2014) e populações (Cadrin et al., 2014; Hüssy et al., 2016). Condições ambientais alteram primariamente a taxa de crescimento dos otólitos, que por sua vez modificam as configurações de formato dos otólitos (Cardinale et al., 2004; Mosegaard et al., 1988; Vignon e Morat, 2010). A variação intrapopulacional na forma dos otólitos pode ocorrer na ausência de diferenças genéticas ou em adição ao componente genético que pode agir sinergicamente com as características fenotípicas (Berg et al., 2018; Cardinale et al., 2004). A extensão em que as diferenças de formato dos otólitos são induzidas genética ou ambientalmente permanece incerta (Cardinale et al., 2004), entretanto, a análise do formato do otólito tem sido usada com sucesso para discriminar os estoques pesqueiros (Campana e Casselman, 1993; Ferguson et al., 2011; Libungan et al., 2015; Bacha et al., 2016; Hüssy et al., 2016).

Os princípios e premissas analíticas da morfometria são similares aos seguidos na microquímica (Eldson et al., 2008; Cadrin et al. 2014; Hüssy et al., 2016; Tanner et al., 2016). Todavia, diferente da química dos otólitos que permite verificar períodos específicos de vida em função da natureza cronológica dos anéis de crescimento, na morfometria dos otólitos a expressão fenotípica é única e resultante de todo o ciclo de vida do indivíduo (Ferguson et al., 2011). Desta forma, muitas vezes as análises químicas elementares encontram estruturações onde a morfometria não visualiza, devido ao espectro temporal específico adotado na metodologia (Begg e Waldman, 1999; Ferguson et al., 2011; Miyan et al., 2016). Porém, essa característica analítica não é uma desvantagem, uma vez que a aplicação de abordagens holísticas com diferentes escopos espaços-temporais é bem-vinda para a ratificação de resultados e visualização da estrutura populacional (Avigliano et al., 2017).

O uso da forma dos otólitos aplicado à diferenciação de estoques pesqueiros tem sido empregado há várias décadas (Templeman e Squire, 1956; Yefanov e Khorevin, 1979; Cadrin et al., 2014; Jemaa et al., 2015; Morales-Nin e Geffen, 2015). Entretanto, os avanços tecnológicos recentes na aquisição, processamento e análise de imagens digitais em softwares

específicos possibilitaram maior complexidade nas medições e cálculos envolvidos, conduzindo a um aumento expressivo na aplicação desta ferramenta considerada de baixo custo em relação a outras de mesma finalidade (Lombarte e Tuset, 2015; Hüssy et al., 2016; Bacha et al., 2016). Atualmente, a variabilidade da forma dos otólitos entre populações tem sido analisada principalmente de três formas: (i) com a tomada de medida do comprimento, largura e perímetro para o cálculo de índices morfométricos (circularidade, retangularidade, elipsidade, fator de forma e arredondamento) (Tuset et al., 2003; Avigliano et al., 2017); (ii) análises Elípticas de Fourier (Libungan e Pálsson, 2015; Hüssy et al., 2016); e (iii) análises geométricas a partir de marcos anatômicos (Wong et al., 2016). O uso conjunto de índices morfométricos e análises de Fourier ou análises geométricas, são provavelmente as duas abordagens de maior sucesso na identificação de populações e/ou estoques pesqueiros (Hüssy et al., 2016; Bacha et al., 2016; Wong et al., 2016).

OBJETIVOS E HIPÓTESES DE PESQUISA

O objetivo geral da tese foi avaliar a estrutura populacional, os padrões migratórios e a conectividade de *Chaetodipterus faber* no Oceano Atlântico Sul. Os objetivos específicos foram enumerados e elencados de acordo com a sequência dos capítulos. Os objetivos específicos (OE) são apresentados abaixo com suas respectivas hipóteses (H) e corolário (C), sendo:

OE 1A) Validar a deposição dos anéis de crescimento anuais nos otólitos sagittae de *Chaetodipterus faber* no Complexo Estuarino de Paranaguá e região costeira adjacente; H1A) A deposição de zonas opacas nos otólitos é anual e associada ao aumento da temperatura; C1A) Se a hipótese for verdadeira, o incremento marginal dos otólitos irá apresentar menores valores na primavera e progressivo aumento nos meses subsequentes.

OE 1B) Realizar estimativas de idade da população coletada no Complexo Estuarino de Paranaguá e região costeira adjacente e avaliar a adequação dos dados de comprimento-idade aos modelos de crescimento de von Bertalanffy, Gompertz e Logístico; H 1B) O crescimento da espécie não apresenta padrão Sigmoidal; C 1B) Se a hipótese for verdadeira, a função de von Bertalanffy descreve melhor o crescimento individual da espécie.

OE 1C) Avaliar a proporção sexual mensal e por classe de tamanho da população no Complexo Estuarino de Paranaguá e região costeira adjacente; H1 C) A proporção mensal e por classe de tamanho de macho:fêmea não é significativamente diferente de 1:1; OE 1C) Se a hipótese for verdadeira machos e fêmeas sofrem pressões ambientais similares ao longo da vida.

OE 1D) Avaliar a dinâmica e a biologia reprodutiva da população no Complexo Estuarino de Paranaguá e região costeira adjacente; H 1D) A população realiza desovas parceladas durante a primavera e verão; C 1D) Se a hipótese for verdadeira a avaliação histológica irá mostrar o recrutamento de ovócitos ao crescimento secundário (vitelogênico) ao longo do ciclo reprodutivo e maiores frequências de machos e fêmeas capazes de desovar na primavera e verão.

OE 1E) Estimar a idade e o comprimento de primeira maturação de machos e fêmeas de *Chaetodipterus faber* no Complexo Estuarino de Paranaguá e região costeira adjacente; H 1E) Os padrões observados são similares ao observados na população subtropical do Atlântico Norte; C 1E) Se a hipótese for verdadeira machos atingem a primeira maturação antes que as fêmeas, com tamanho de 10 cm e um ano de idade.

OE 2) Avaliar a estrutura populacional de *C. faber* no oceano Atlântico Sudoeste com recurso ao uso das assinaturas químicas elementares (elemento/cálcio) e da forma dos otólitos; H 2a) Diferentes populações ocorrem no oceano Atlântico Sudoeste e são diferenciadas pela assinatura química e da forma dos otólitos; C 2a) Se a hipótese for verdadeira, a variabilidade geográfica reflete-se na variação espacial da composição química e na forma dos otólitos de *C. faber*.

OE 3) Analisar o uso obrigatório de áreas estuarinas como berçários de *C. faber* em diferentes latitudes da costa brasileira por meio dos registros químicos (Sr/Ca, Ba/Ca e Mn/Ca) gravados em diferentes seções transversais dos otólitos; H 3a) Menores taxas de Sr/Ca e maiores taxas de Ba/Ca e Mn/Ca estão presentes nas seções dos otólitos referentes a sua fase juvenil (núcleo do otólito) em detrimento da borda do otólito que representa o momento de captura; C 3a) Se a hipótese for verdadeira habitats estuarinos podem ser considerados berçários efetivos para a espécie e adicionalmente os transectos das razões elemento/Ca ao longo dos otólitos irão permitir inferências sobre o padrão migratório da espécie. H 3b) Elevados valores de Sr/Ca e baixos valores de Ba/Ca e Mn/Ca são verificados do núcleo a borda dos otólitos; C 3b) Parte da população é residente em água salgada durante todo o seu ciclo de vida.

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CAPÍTULO 2

Age, growth, and reproductive biology of the Atlantic spadefish *Chaetodipterus faber* in southern Brazil

Age, growth, and reproductive biology of the Atlantic spadefish *Chaetodipterus faber* in southern Brazil

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Abstract This is the first study to investigate the age, growth and reproductive biology of the Atlantic spadefish *Chaetodipterus faber* in southern Brazil. A total of 625 individuals [total length (TL) ranging from 7 mm to 510 mm] were sampled at the Paranaguá Estuarine Complex (PEC) and adjacent coastal areas over a year (August 2015 to July 2016). Age estimation based on sagittal otoliths cross-section showed that *C. faber* has a 17-years longevity close to its southern distributional limit, two times greater than previously reported from the North Atlantic. Sexual growth dimorphism was not evident as the male:female sex ratio was 1:1.17. The species displayed asymptotic growth. Fitted von Bertalanffy growth function estimates for all individuals were L_∞ = 508.81 mm, k = 0.22 year^{-1}, and t_0 = -0.05 year. The histological gonadal examination and gonado-somatic index indicated that *C. faber* is a batch spawner with a main reproduction period from October to January in subtropical latitudes at 25°S. Postovulatory follicles were often recorded in the ovaries of spawning capable individuals indicating a high frequency of spawns over the reproductive period. The data also suggest that estuaries are important reproductive areas for this species that most likely exhibits a seasonal movement for spawning aggregation purposes. Females mature approximately 0.5 years later than males and are capable of spawning just prior to two years old. Fishery closures during the spawning season and fishing size restrictions should be used to manage the *C. faber* stock in southern Brazil. The effects of current harvest levels are unknown and warrant further investigation to assist management decisions.

Keywords Ephippidae · Growth modelling · Reproduction · Sexual maturity · South Atlantic

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Introduction

The Ephippidae family comprises eight genera and 15 species distributed in coastal environments of the subtropical and tropical regions of the Indian, Pacific and Atlantic Oceans (Nelson 2006; Eschmeyer and Fong 2018). The only species that occurs along the western Atlantic Ocean is the Atlantic spadefish *Chaetodipterus faber* (Broussonet 1782). The species is distributed from Massachusetts (United States) to Santa Catarina, South Brazil, encompassing the Caribbean Sea and Gulf of Mexico (Burgess 2002; Soeth et al. 2014; Machado et al. 2017). In subtropical regions of the North Atlantic *C. faber* males and females exhibit early maturation at around 1 year old (Hayse 1990). The species is a pelagic spawner (Chapman 1978; Ditty et al. 1994) that forms reproductive aggregations that have been recorded during underwater observations (Chapman 1978; Heyman and Kjerve 2008). Pelagic larvae occur primarily in coastal waters and begin their transition to the juvenile stage after 25 days when individuals reach 8.0 to 8.5 mm standard length (Ditty et al. 1994; Castro et al. 2005). Demersal early juveniles are plant-mimetics (Barros et al. 2015) and common in estuarine and coastal regions (Barros et al. 2013; Soeth et al. 2014; Possato et al. 2016). Adults change to a benthopelagic behavior and are known to be a reef-associated fish, frequently observed on rocky reefs, artificial reefs and other consolidated continental shelf structures up 30 meters deep (Hayse 1990; Burgess 2002; Simon et al. 2013; Daros et al. 2012). *Chaetodipterus faber* can reach over 6 kg in total mass (IGFA 2017) with longevity of at least 8 years (Hayse 1990). The species exhibits trophic plasticity throughout their life cycle, feeding on algae, benthic epifauna and planktonic cnidarians (Hayse 1990; Barros et al. 2013). *Chaetodipterus faber* is also an important food source for top predators such as *Tursiops truncatus* (Gurjão et al. 2004), *Epinephelus itajara* (Gerhardinger et al. 2006), and *Galeocerdo cuvier* (Bornatowski et al. 2007).

The Atlantic Spadefish recreational fisheries have grown in popularity and developed into a specialized and directed fishery in the United States waters (Bell 2005). In Brazil, *C. faber* is highly targeted by recreational fisheries (Pinheiro et al. 2010) but total catch is dominated by artisanal and industrial fleets that have landed around 250 tons per year along the Brazilian coast for the past decade (IBAMA 2007; MPA 2012). The species often congregates in large schools in coastal waters (Burgess 2002), mainly in the spring and summer at subtropical latitudes, which greatly increases its potential for harvest (Bell 2005; PMAP-BS 2017a, 2017b). However, these aggregation periods appear to coincide with the peak spawning season for *C. faber* (Hayse 1990; Castro et al. 2005), which makes the species

vulnerable to demographic over-exploitation (Sadovy de Mitcheson et al. 2008; Sadovy de Mitcheson and Colin 2012; Chao et al. 2015). Additionally, the decline of many fish population globally (Myers and Worm 2003) has led to a gradual transition in fisheries landings from long-lived, high-trophic level fishes, toward short-lived and low trophic level fishes (Pauly et al. 1998). In southern Brazil, this scenario is not different. The average annual industrial landings of *C. faber* has increased by 6 times, from 36 tons in 2000 and 2011 to 240 tons from 2012 to 2017 (UNIVALI/CTTMar 2010, 2013a, 2013b, PMAP-SC 2018). The schooling behaviour makes *C. faber* particularly vulnerable to purse seine vessels, typically used in the herring and mackerel fisheries (Misund 1993; PMAP-SC 2018). Currently there is no specific legislation to prevent the use of purse seine nets to target *C. faber* aggregations.

Fish life-history traits, including growth, maturity, and reproduction, are extremely diverse and species specific (Pauly 1980; Vazzoler 1996); understanding these traits is integral to the successful fisheries management and conservation of exploited fishes (Harry et al. 2013; van Overzee and Rijnsdorp 2014; Aschenbrenner et al. 2017). For instance, information about size at maturity and the timing of reproductive events can be used as biological reference points for management decisions on size limits and periodic fishery closures during spawning seasons (Yamahira 2004; Lowerre-barbieri 2009; van Overzee and Rijnsdorp 2014). In addition, length and age composition data are essential to the estimation of biological parameters including growth rates and natural mortality, which are fundamental to modelling population and biomass dynamics (Pauly 1980; Wartenberg et al. 2013; He et al. 2016; Aschenbrenner et al. 2017). However, biological and ecological information regarding population structure, feeding regimes and migratory behavior for *C. faber* in the SW Atlantic is scarce (Barros et al. 2013, 2015; Machado et al. 2017). Estimates of key life-history parameters are unknown for this region.

The objective of this study was to provide life-history information critical to the successful management of the *C. faber* stock in southern Brazil. The aims of this study were to (1) estimate individual fish ages based on sagittal otolith cross-sections, (2) model population growth, (3) determine size frequency distributions and sex compositions, (4) determine reproductive cycles using histological analysis of gonads and the gonado-somatic index, and (5) estimate the size- and age-at-maturity for *C. faber* males and females.

Materials and methods

Study area and biological sampling. Fish sampling took place monthly between August 2015 and July 2016 at the Paranaguá Estuarine Complex (PEC) (25°30'S, 48°25'W) and adjacent coastal areas of the Paraná state, southern Brazil (Fig. 1). The PEC is characterized by a range of habitats including mangrove forests, tidal flats, tidal creeks, rivers, estuarine beaches, rocky reefs, and deep channels (Lana et al. 2001). The adjacent inner shelf is dominate by sandy-bottom (> 99 %) and includes scattered rocky reefs, artificial reefs and islands (Veiga et al. 2004; Brandini 2014). The study area has a humid subtropical climate with an annual average rainfall of 2,500 mm (Lana et al. 2001), wet summers and dry winters, and subsurface water temperature varying from 18°C to 28°C (Soeth et al. 2015).

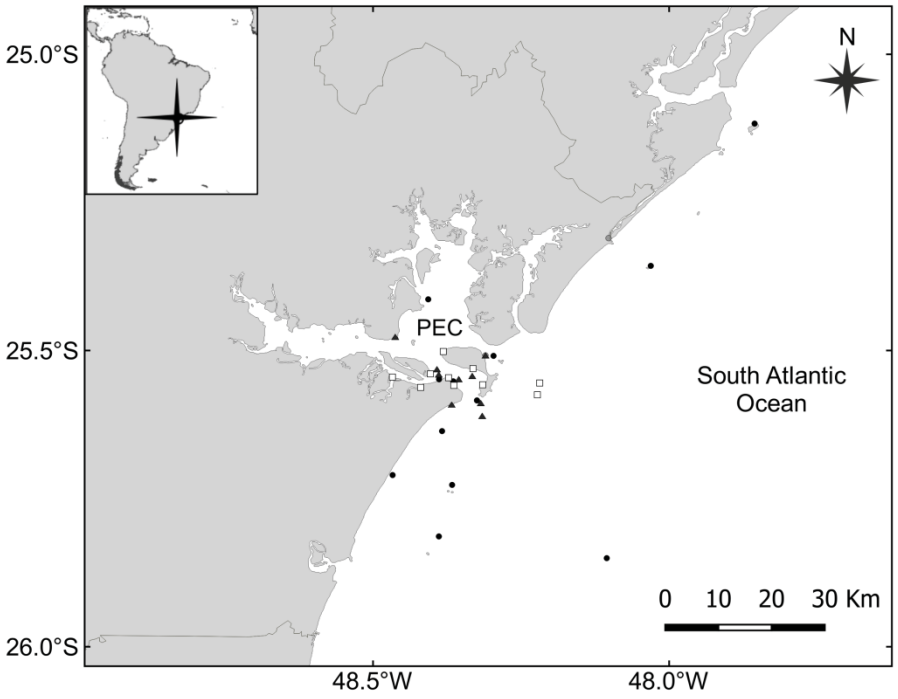

Fig. 1 Sampling location of *Chaetodipterus faber* caught in the Paranaguá Estuarine Complex (PEC) and adjacent coastal areas from August 2015 to July 2016 by spearfishing (black circles), seine nets (white squares) and acquisition from local fishermen (gray triangles)

A total of 625 individuals were sampled (Table 1) using multiple gear types to provide a representative sample across size and age groups. About 50 % of the total (i.e., 307 individuals) were sampled by spearfishing that required approximately 10 hours per month of freediving effort on rocky reefs, artificial reefs and in marinas or around anchored ships in the study area. Additionally, seine nets were used in tidal estuarine beaches of the PEC; bimonthly from August 2015 to June 2016 with a 70 m x 2 m seine net and stretched mesh

size of 2 cm (4.16 % of individuals); and monthly from January to July of 2016 with 15 m x 2 m seine net and stretched mesh size of 2 mm (16.29 % of individuals). Finally, remaining samples were obtained from local fishermen that used trammel and gill nets with stretched mesh sizes ranging from 90 mm to 250 mm (26.43 % of individuals) or demersal penaeid trawls (4 % of individuals).

Table 1 Sample size (n), mean, minimum (Min) and maximum (Max) total length (millimeters) and sex ratio (Males:Females, M:F) by month for *Chaetodipterus faber* caught in the Paranaguá Estuarine Complex and adjacent coastal areas from August 2015 to July 2016

Date		*n*	Mean	Min	Max	M:F
2015	August	54	181	134	510	1:0.82
	September	54	167	96	323	1:1.17
	October	30	288	73	508	1:1.42
	November	37	286	146	486	1:0.85
	December	104	306	84	493	1:1.46*
2016	January	63	174	20	479	1:1.06
	February	42	212	24	473	1:1.06
	March	71	161	7	380	1:1.20*
	April	37	179	18	445	1:1.17
	May	56	83	12	297	1:1.29
	June	43	145	24	400	1:1
	July	34	148	31	348	1:1.50

Superscript * indicates significant differences ($\chi^2 < 3.840$, $d.f. = 1$, $P < 0.05$) observed by χ^2 test

Upon collection, fish were immediately preserved on ice and transported back to the laboratory for processing. All fish were measured for total length (TL, 1 mm), weighed (0.01 g) for total fish mass (TM), gonad mass (GM), and gutted fish mass (GFM). Sagittal otoliths were removed, cleaned of adherent tissues and stored dry in labeled Eppendorf tubes. The gonads were initially evaluated macroscopically for sex determination and development stages, which were later confirmed by routine histological analysis (see Reproductive biology section).

Sex ratio and mass-length relationship. Sex ratio was calculated by month and for each 50 mm TL size class according to Sturges rules (Sokal and Rolf 1981). Significant monthly deviations from the expected 1:1 sex ratio were determined by a χ^2 test ($\chi^2 < 3.840$, *d.f.* = 1, $P < 0.05$) for each class. The sex-specific mass-length (grams-millimeters) relationship was calculated by the equation: $TM = aTL^b$ where *a* is the linear coefficient and *b* is the slope (Le Cren 1951). The r-squared (r^2) values, in conjunction with residual plots, were used to assess the how well the model fitted the dataset. The mass-length relationship of males and females were compared using analysis of covariance (ANCOVA) in R (R Core Team 2017).

Age determination and validation. Age estimation of transverse otolith cross-sections were made using an established protocol for *C. faber* (Davies et al. 2015). Left otoliths were embedded in transparent epoxy resin, and were cut near the nucleus (0.5 mm) with a Buhler Isomet Low-Speed Saw. Otolith cross-sections were ground along the transverse plane to expose the core with 400, 1,200 and 2,400 silicon carbide papers and further polished with alumina paste. Thereafter thin sections were immersed in a clearing agent (alcohol: glycerin, 1: 1) for 48 hours. Microphotographs were obtained using a microscope with transmitted light coupled to a 5 megapixels Opticam (OPT5000 Power) at 40x magnification.

All cross-sections were blind-counted (i.e., without the knowledge of capture date and fish size) three times by one experienced reader. Repeated readings were done with a minimum fifteen day interval. Otoliths that showed discrepancies between counts were re-aged and the final age was assigned when at least two counts agreed. To improve the age estimation, the average radius from otolith cross-sections of late young-of-the-year was used to determine the expected radius (1 mm) of the first annulus (Campana et al. 2001; Natanson et al. 2002). Individual age estimates for *C. faber* were assigned based on the opaque zone counts, starting from the nucleus towards the proximal edge, taking into consideration the date of capture and the assumed birth date for this population based on the peak spawning season identified in the results (Morales-Nin and Panfili 2002; Davies et al. 2015). The average coefficient of variation index (ACV) and the average percent error (APE) were calculated to measure precision among age estimates (Beamish and Fournier 1981; Chang 1982; Ogle 2016).

Analyses of edge-type (expressed as percentage of opaque or translucent otolith edge) and the relative marginal distance (RMD) were used to validate the annual growth pattern increment deposition based on Panfili and Morales-Nin (2002). The quantification of the

RMD was calculated according to the formula: $RMD = MD(LA)^{-1}$, where MD was distance that separated the last opaque band from the edge of the otolith, and LA was the width of the last complete annulus. Fish age groups 0 and 1 and older than 5 were excluded from the RMD and edge-type analyses due to the difficulty in calculating the RMD for the age 0 group, the difficulty in visualizing the first annuli for the age 1 group and the low monthly frequency of older individuals. Otoliths with poor legibility of annuli (16.5 %) were also disregarded in these analyses (Aschenbrenner et al. 2017). Otolith measurements were taken using the software ImageJ (IJ 1.46r version). A non-parametric Kruskal–Wallis one-way ANOVA, followed by pairwise comparisons using Fisher's least significant difference test, were used to identify differences among monthly mean RMD (Conover 1990).

Age and growth. The age-at-length dataset contained data for males, females, and all individuals pooled. Three length-at-age models were evaluated for goodness of fit: the von Bertalanffy growth function (VBGF), the Gompertz growth model (GM), and the Logistic model (LM) (Ogle 2016). The VBGF was fitted by the equation: $L_t = L_\infty\left[1 - e^{-k(t - t_0)}\right]$, where L_t is the TL (mm) as a function of a given age, L_∞ is the theoretical asymptotic TL mm, k is the growth coefficient ($year^{-1}$), t_0 is the theoretical age (years) at which the length is zero. The GM was given by the function: $L_t = L_\infty e\left[- e^{-gi(t - ti)}\right]$, where gi is the instantaneous growth rate ($year^{-1}$) at the inflection point, ti is the age (years) at the inflection point. The LM was: $L_t = L_\infty[1 + gninf(t - ti)]^{-1}$, where $gninf$ is the instantaneous growth rate ($year^{-1}$) at negative infinity. A bootstrap method with 1000 iterations was applied to estimate the 95 % confidence intervals (C.I.) of the parameters. Akaike Information Criterion (AICc) was used to assess the best-fit model based on goodness of fit and parsimony for males, females and all individuals pooled (Hurvich and Tsai 1989). The model with the smallest AICc value was selected as the best among the candidates. The AICc difference (ΔAICc or Δ_i) were computed for candidate models to evaluate relative model support. Models with $\Delta_i < 2$ have substantial support, while there is considerably less support for models with $4 < \Delta_i < 7$ and models with $\Delta_i > 10$ have essentially no support and might be omitted from further consideration (Burnham and Anderson 2002). The likelihood ratio and extra sum-of-squares tests were used to compare results between VBGF parameters for males and females (Kimura 1980; Ritz and Streibig 2008; Ogle 2016). All age and growth analyses were performed using the *Agricolae, FSA*, *nlstools*, and *AICcmodavg* packages loaded into R (R Core Team 2017).

Reproductive biology. The gonado-somatic index (GSI) was calculated according to the formula: $GSI = [GM(GFM)^{-1}]100$. The transformation [Log(GSI + 1)] was unsuccessful in transforming the data to a state of normality and homogeneity of variances. Thus, a non-parametric Kruskal–Wallis one-way ANOVA tests, followed by pairwise comparisons using Fisher's least significant difference, were used to compare differences among monthly GSI means for adult males and females (Conover 1990).

For microscopic determination of development stages, the gonads were fixed in ALFAC, embedded in paraffin wax and sectioned at 5-7 μm. Slides were stained with haematoxylin-eosin and analyzed under a compound light microscope (Vazzoler 1996) in order to assign sex and reproductive phase: immature (phase I), developing [subphase early developing (II) and late developing (III)], spawning capable (IV), actively spawning capable subphase (V), regressing (VI), and regenerating (VII) (Brown-Peterson et al. 2011). Individuals with very small gonads (< 0.001 g) were considered as indeterminate since it was impossible to identify the sex and reproductive phase. The relative frequency distribution of each reproductive phase was calculated by month and analyzed together with the GSI to confirm the spawning season.

Maturity ogives were used to estimate the length- (L_{50} and L_{95}) and age- (A_{50} and A_{95}) at- maturity as the TL and age at which 50 % and 95 % of the males and females were mature. Maturity stages were converted to binary maturity determinations (0 = immature, 1 = mature). The following logistic regression model was used to estimate length- and age-at-maturity for males and females as: $PM = PMAX[1 + e^{-\ln(19)\{(1-\beta_1)(\beta_2-\beta_1)^{-1}\}}]^{-1}$, where PM is a proportion of mature at TL or age; β_1 and β_2 are fitted parameters corresponding to L_{50} and L_{95} or A_{50} and A_{95}, respectively; PMAX is the asymptote (Harry et al. 2013). A bias-reduction generalized linear model with binomial responses and logit-link (Kosmidis 2014) was used to estimate parameters β_1 and β_2 (Harry et al. 2013). A bootstrap method with 1000 iterations was applied to estimate the 95 % C.I. The presence of cortical alveoli oocytes was considered as an indication that *C. faber* was sexually mature and would spawn during that reproductive season (Brown-Peterson 2003). Therefore, only immature individuals (phase I) were not considered adult (Brown-Peterson et al. 2011; Lowerre-Barbieri et al. 2011). Individuals collected outside of the reproductive, period when there were higher percentages of regenerating females, were excluded from maturity determination analysis (Hunter and Macewicz 2003; Lowerre-Barbieri et al. 2011). For immature fish smaller than 45 mm TL, for which sex was indeterminate, a double entry (once as female and then again as male) was added to the

dataset used to construct maturity ogives (Boulcott et al. 2007). All reproductive analyses were performed using the *Agricolae, MASS*, *psyphy*, *brglm*, and *boot* packages loaded into R software (R Core Team 2017).

Results

Sample composition, sex ratio, and mass-length relationships. From the total of 625 *Chaetodipterus faber* samples, 274 were females, 237 were males and 114 individuals were indeterminate. Female TL ranged from 68 mm to 510 mm (mean TL 245 ± SD 120 mm), male TL ranged from 41 mm to 508 mm (mean TL 224 ± SD 110 mm), and indeterminate TL ranged from 7 mm to 48 mm (mean TL 28 ± SD 10 mm). The male:female sex ratio was 1:1.17 and did not differ significantly from the expected ratio of 1:1 ($\chi^2 = 2.69$; $P > 0.05$). The proportion of females was higher than males only in the 450–499 mm TL size class ($\chi^2 = 5.95$; $P < 0.05$) (Fig. 2). The sex ratio differed significantly from the expected 1:1 sex ratio in December ($\chi^2 = 5.96$; $P < 0.05$) and March ($\chi^2 = 4.36$; $P < 0.05$), where female dominance was recorded. Males and females demonstrated negative allometric growth and mass-length relationships were not significantly different between males $TM = 0.00009\ TL^{2.829}$ (n = 237; $r^2 = 0.990$) and females $TM = 0.0001\ TL^{2.811}$ (n = 274; $r^2 = 0.993$) (ANCOVA, $F = 0.488$; $P > 0.05$). Therefore, the relationship for pooled sexes was $TM = 0.00009\ TL^{2.821}$ (n = 511; $r^2 = 0.991$). In contrast, indeterminate individuals demonstrated positive allometric growth where $TM = 0.000007\ TL^{3.404}$ (n = 114; $r^2 = 0.992$).

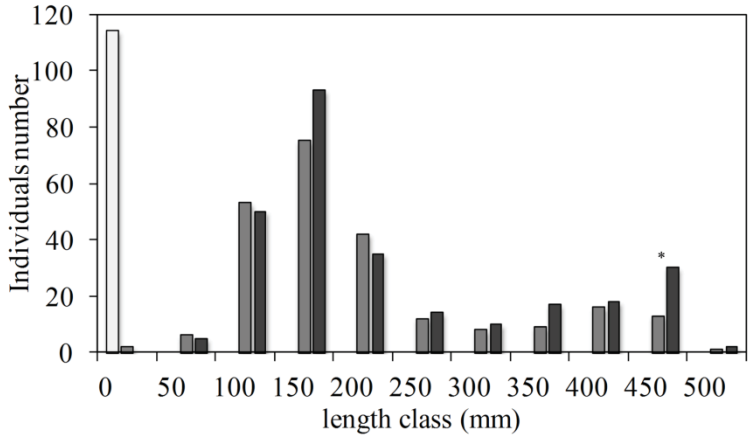

Fig. 2 Individuals number of *Chaetodipterus faber* with indeterminate sex (□), males (■), and females (■), by length classes, caught in the Paranaguá Estuarine Complex and

surrounding areas in southern Brazil from August 2015 to July 2016. Superscript * indicate significant differences ($\chi^2 < 3.840$, *d.f.* = 1, $P < 0.05$) observed by χ^2 test

Age determination and validation. The average coefficient of variation and the average percent error among age estimates was 3.07 % and 2.36 %, respectively. From the 625 *C. faber* samples, 90 % (562 individuals) were aged successfully. The remaining otoliths were discarded due to the variability in readings or because they were damaged during processing.

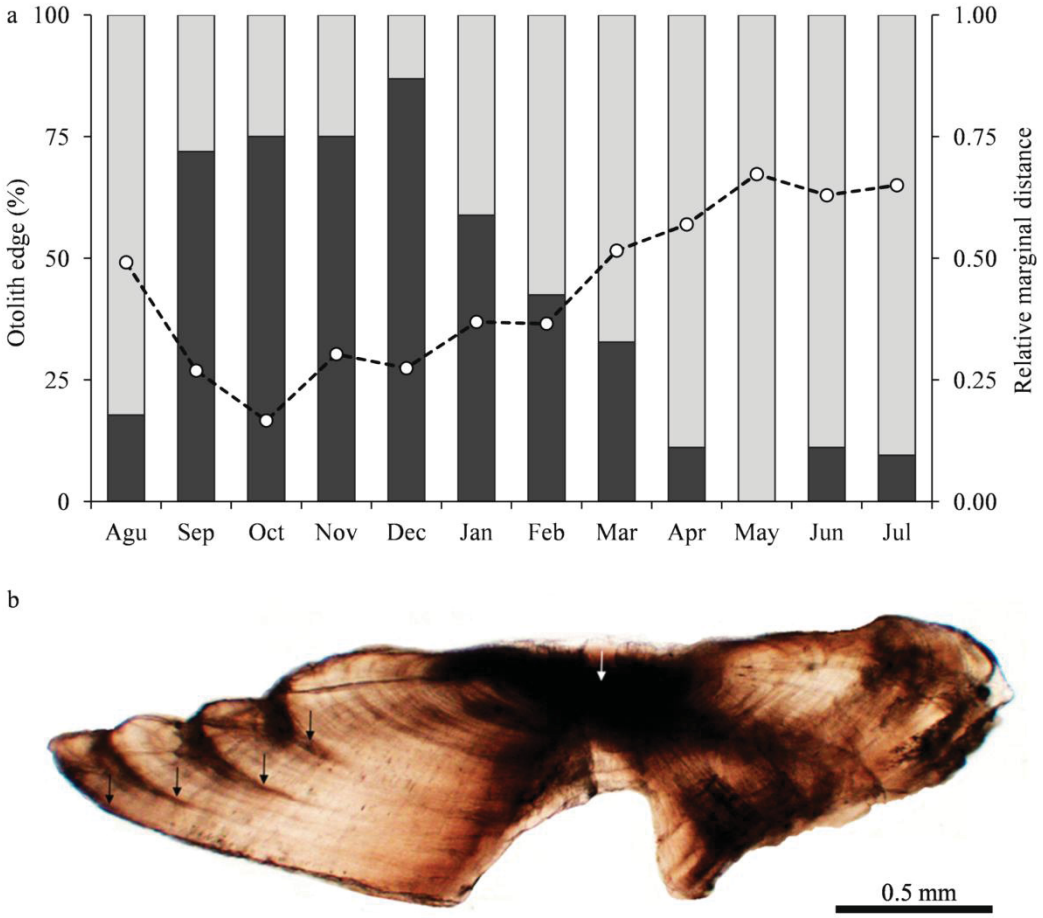

Fig. 3 (**a**) Monthly edge-type analysis expressed as percentages of opaque (■) or translucent (□) otolith edges and average monthly relative marginal distance (RMD) (line and open circles) for *Chaetodipterus faber* (age 2 to 5 years pooled; n = 167) collected from the Paranaguá Estuarine Complex and surrounding areas from August 2015 to July 2016. (**b**) Transverse sections from the left sagittal otolith of a four-year old *C. faber* (TL = 227 mm) collected in December 2015 from the Paranaguá Estuarine Complex. *dark arrows* Annuli (opaque zones), *white arrow* nucleus. Image viewed at 40x Magnification

The Kruskal–Wallis test indicated significant differences in the RMD between months (Kruskal–Wallis $H = 89.39$; $P < 0.001$). The lower median RMD from September 2015 to December 2015 ($P < 0.05$) suggests that opaque bands are laid down during these months when higher proportions of opaque otolith edges were recorded. In May 2016, 100 % of the otolith edges were translucent. These results suggest that a single opaque zone is deposited each year (Fig. 3a). The deposition of the opaque bands was accompanied generally by a depression at the distal margin of the otoliths (Fig. 3b).

Age and growth. Age estimates from otoliths ranged from 0 to 17 years (Table 2). Individuals older than 11 years were rare and the oldest fish was a male of 508 mm TL sampled from the coastal beach adjacent to the PEC. The longest TL was 510 mm from a female of 10 years old caught inside the PEC. Although the growth models demonstrated some support ($\Delta_i < 2$), prediction varied according to the dataset and the model used. The VBGF exhibited the lowest AICc for males and all individuals pooled, while the GM exhibited the lowest AICc for females (Fig. 4; Table 3). The age at the inflection point (*ti*) for the GM was higher for females (1.96 years) than males (1.83 years). The LM was only suitable as an alternative model for modeling growth in females ($\Delta_i = 0.47$; $\omega i = 0.4$). The inclusion of small individuals in the pooled dataset produced more realistic t_0 estimates that were closer to 0, conferring a bias reduction by the addition of these fish in the analyses (Table 3). Additionally, *k*, *gi* and *gninf* were higher in this dataset. Despite the different support levels exhibited by the AICc between males ($\Delta_i = 0$) and females ($\Delta_i = 3.53$), mean VBGF parameter estimates were compared between sexes. There were no significant differences in L_{∞}, k, and t_0 beteween males and females as shown by the likelihood ratio test ($\chi^2 = 5.60$; $P > 0.05$) and extra sum-of-squares test ($F = 1.853$; $P > 0.05$).

Table 2 Age-length distribution for all *Chaetodipterus faber* caught in southern Brazil from August 2015 to July 2016

TL (mm)	Age (years)																	
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
0 - 49	107																	
50 - 99	7	5																
100 - 149	18	86	2															
150 - 199		71	53	11	4	1	1											
200 - 249		9	30	10	8	6	1											
250 - 299			16	3	1			1	1									
300 - 349			5	4	2	1			1	1								
350 - 399				7	11	4	1		1									
400 - 449			1	3	5	6	8	3	2	1	1							
450 - 499					1	5	2	4	3	10	7	4	1			2		
500 - 549											1				1			1
Total	132	171	107	38	32	23	13	8	8	12	9	4	1	0	1	2	0	1

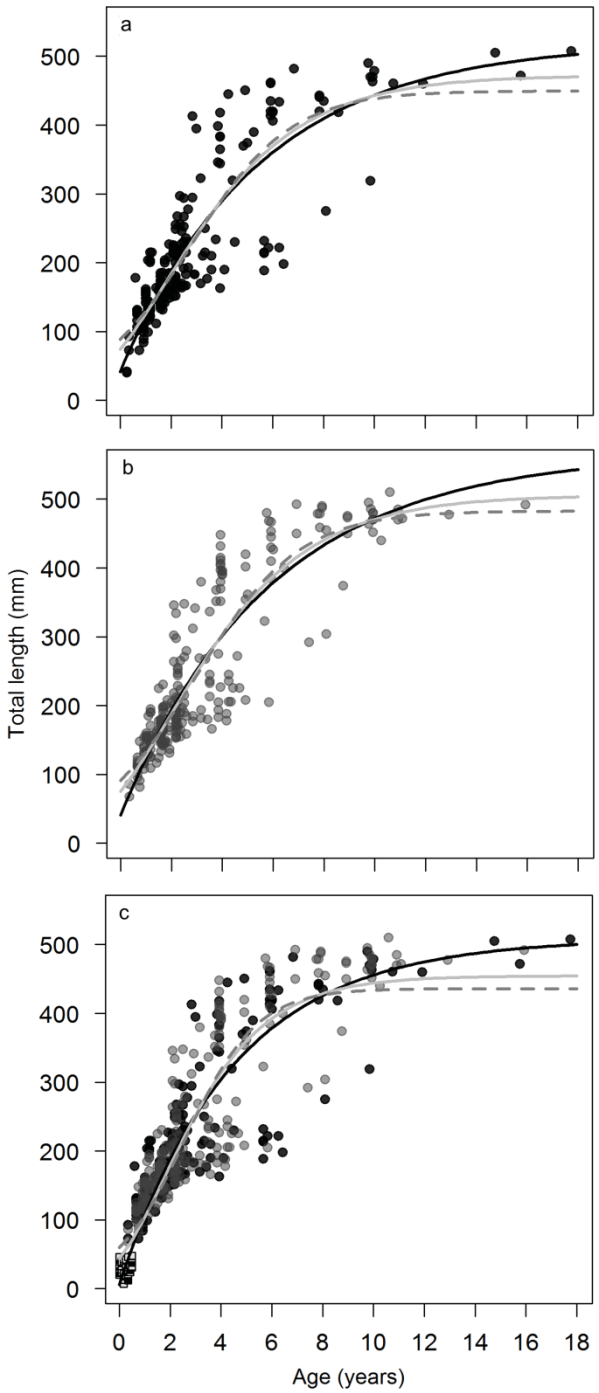

Fig. 4 Age-at-length plot for *Chaetodipterus faber* (**a**) males (n = 215), (**b**) females (n = 243), and (**c**) all individuals (n = 562) collected from the Paranaguá Estuarine Complex and surrounding areas from August 2015 to July 2016. In each plot the von Bertalanffy growth model (solid black line), Gompertz model (solid gray line) and Logistic model (dashed gray line) are showed. Points depict individual fish by age; males (●), females (●), and individuals with indeterminate sex (□)

Table 3 Estimated von Bertalanffy growth function (VBGF), Gompertz model (GM), and Logistic model (LM) parameters describing the length-at-age relationship of *Chaetodipterus faber* males, females, and all individuals pooled. Logistic regression models (LRM) for the estimated proportion of mature *C. faber* relative to total length and age are also presented. Samples were collected from the Paranaguá Estuarine Complex and surrounding areas in southern Brazil from August 2015 to July 2016.

		Males		Females		All individuals	
Model	Parameter	Estimates	C.I.	Estimates	C.I.	Estimates	C.I.
VBGF	L_∞ (mm)	520.87	466 - 598	567.2	509 - 664	508.81	483 - 537
	K (year^{-1})	0.18	0.13 - 0.24	0.17	0.12 - 0.22	0.22	0.20 - 0.25
	t_0 (year)	-0.46	-0.84 - -0.13	-0.44	-0.86 - -0.12	-0.05	-0.15 – 0.05
	AICc	2330.04		2641.16		6032.91	
	Δ_AICc	0		3.53		0	
GM	L_∞ (mm)	472.12	436 - 516	505.72	470 - 548	454.57	438 – 473
	gi (year^{-1})	0.34	0.27 - 0.41	0.33	0.27 - 0.39	0.46	0.42 - 0.51
	ti (year)	1.83	1.58 - 2.18	1.96	1.73 - 2.92	1.85	1.73 - 1.97
	AICc	2331.9		2637.63		6081.67	
	Δ_AICc	1.86		0		48.76	
LM	L_∞ (mm)	449.68	419 - 482	482.81	456 - 516	435.99	421 - 451
	gninf (year^{-1})	0.51	0.43 - 0.60	0.49	0.42 - 0.57	0.71	0.66 - 0.78
	ti (year)	2.78	2.44 - 3.19	2.95	2.66 - 3.35	2.60	2.44 - 2.74
	AICc	2336.89		2638.10		6130.47	
	Δ_AICc	6.85		0.47		98.03	
LRM	L_{50} (mm)	98	91 - 108	144	133 - 158		
	L_{95} (mm)	147	122 -163	204	176 - 214		
	A_{50} (year)	0.89	0.74 - 1.06	1.37	1.11 - 1.62		
	A_{95} (year)	1.79	1.31 - 2.10	2.29	1.51 - 2.63		

C.I. = 95% confident intervals; L_∞ (mm) = theoretical asymptotic TL; k (year^{-1}) = is the growth coefficient; t_0 (years) = theoretical age at which length is zero; AICc = Akaike information criterion; ΔAICc = AICc difference; *gi* (year^{-1}) = instantaneous growth rate at the inflection point; *ti* (years) = is the age at the inflection point; *gninf* (year^{-1}) = is the instantaneous growth rate at negative infinity; L_{50}, L_{95}, A_{50}, A_{95}= TL (mm) and age (years) at which 50 % and 95 % of the individuals were mature

Reproductive biology. Both the monthly GSI average and relative frequency of the developmental sexual phases showed a peak during the reproductive season between October 2015 and January 2016. The GSI averages were significantly different among months for both adult females (Kruskal–Wallis $H = 125.20$; $P < 0.0001$) and males (Kruskal–Wallis $H = 138.44$; $P < 0.0001$) with higher mean values from October 2015 to January 2016 ($P < 0.05$) for both sexes (Fig. 5).

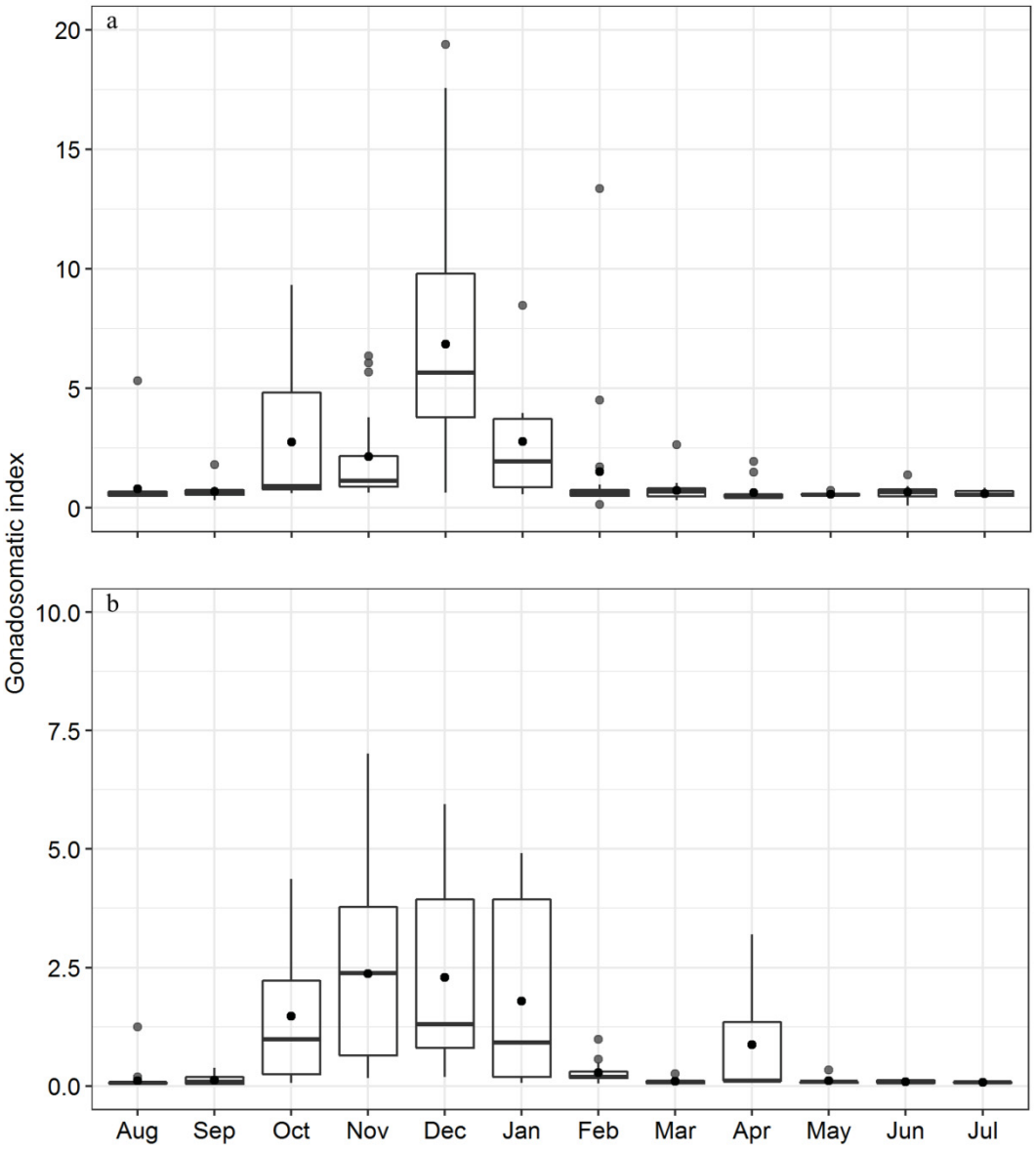

Fig. 5 Box-plot of monthly variation in the gonado-somatic index (GSI) of adult *Chaetodipterus faber* (**a**) females (n = 228) and (**b**) males (n = 211) from the Paranaguá Estuarine Complex and surrounding areas in southern Brazil sampled from August 2015 to July 2016. Dark bands indicate median proportions, box edges indicate the 25 % and 75 % quartiles, whiskers represent maximum and minimum values and samples with values 1.5

times lower or bigger than the quartiles are showed as grey points. Dark points shows monthly averages

The ovarian histological examination demonstrated that *C. faber* sustains a constant reserve of primary growth oocytes throughout all development phases. Asynchronous oocyte development and multiple reproduction phases exhibited monthly within an extended reproduction season suggesting that *C. faber* is a batch spawner (Figs. 6 and 7). Primary oocytes were recruited for secondary growth in September 2015 and October 2015 when the relative frequency of females in the developing phase increased. Individuals in the spawning capable phase increased from October 2015 onwards (Fig. 7). The actively spawning subphase was highest in December 2016 (Figs. 6d and 7), coinciding with highest GSI values collected from the southern region of the PEC. Almost all spawning capable and actively spawning females presented postovulatory follicles (POFs) indicating an elevated spawning frequency at the study site (Fig. 6e). Males were reproductively active (Fig. 6b) slightly longer than females which ceased spawning from January 2016 through to March 2016, as shown by the high relative frequency of regressing individuals (Fig. 6f and Fig. 7).

Immature males TL (n = 14) ranged from 41 mm to 169 mm while immature females TL (n = 39) ranged from 68 mm to 164 mm. All males < 99 mm TL and younger than 0.75 years, and all females < 120 mm TL and younger than 1 year were immature (Fig. 6a, c). The smallest sexually mature male and female were 99 mm and 120 mm TL, respectively. The youngest sexually mature male and female were 1 year old fish. Males reached maturity at smaller size and younger age than females which took approximately 0.5 years longer to reach maturity (Table 3 and Fig. 8).

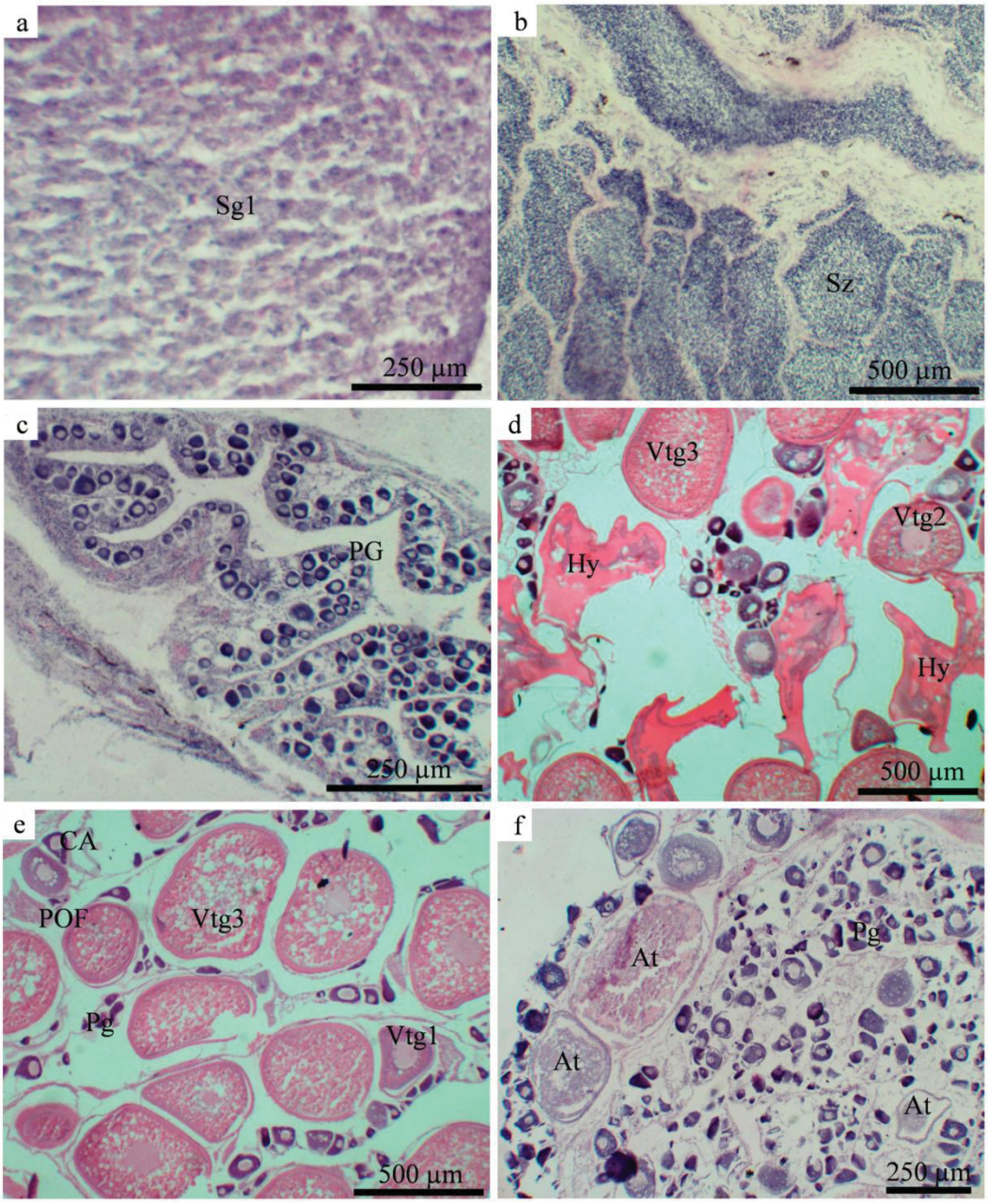

Fig. 6 Microphotographs of gonad histology of *Chaetodipterus faber* collected from the Paranaguá Estuarine Complex and surrounding areas. (**a**) Immature male (TL = 73 mm; GSI = 0.007); (**b**) Spawning capable male (TL = 123 mm; GSI = 0.26); (**c**) Immature female (TL = 68 mm; GSI = 0.12); (**d**) Spawning capable female in active spawning condition (TL = 490 mm; GSI = 10.06); (**e**) Spawning capable female (TL = 464 mm; GSI = 6.98); (**f**) Regressing female (TL = 298 mm; GSI = 0.98). *At* Follicular atresia, *CA* cortical alveolar oocyte, *Hy* hydrated oocyte, *PG* primary growth oocytes, *POF* postovulatory follicle complex, *Sg1* primary spermatogonia, *Sz* spermatozoa, *Vtg1* primary vitellogenic oocyte, *Vtg2* secondary vitellogenic oocyte, *Vtg3* tertiary vitellogenic oocyte

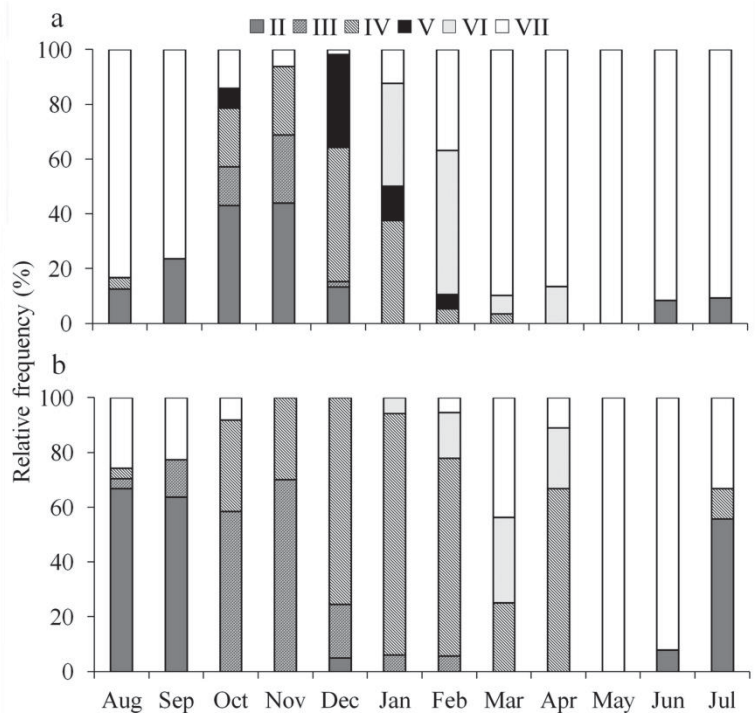

Fig. 7 Relative frequency of each reproductively mature phase and subphases by month for (**a**) females (n = 228) and (**b**) males (n = 211) of *Chaetodipterus faber* caught in the Paranaguá Estuarine Complex and surrounding areas in southern Brazil from August 2015 to July 2016. *II* Early developing , *III* late developing, *IV* spawning capable, *V* actively spawning capable, *VI* regressing, *VII* regenerating

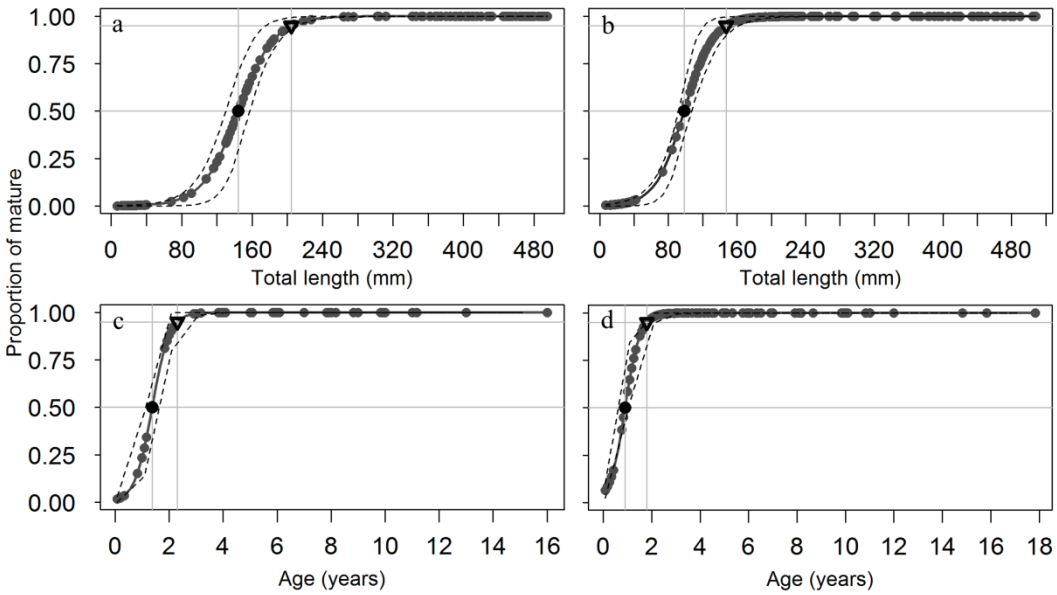

Fig. 8 Mean ± 95% C.I. logistic regression models for the estimated proportion of mature *Chaetodipterus faber* relative to total length for females (**a**) and males (**b**) and relative to the age of females (**c**) and males (**d**) collected at the Paranaguá Estuarine Complex and

surrounding areas in southern Brazil during August 2015 to July 2016. Sample sizes are 109 for females and 192 for males. Dark points and triangles indicate L_{50} and A_{50} and L_{95} and A_{95}, respectively

Discussion

This is the first study that provides information on age, growth and reproduction of *Chaetodipterus faber* in the South Atlantic Ocean. As previously recorded by Hayse (1990), no significant gender differences were found in the sex ratio of sampled population, despite the slight deviation in favor of females which is common in gonochoric fishes (Tsikliras et al. 2010). However, the proportion of females significantly outnumbered males in the 450 to 499 mm TL size class. This pattern was not consistent across months because it was observed in December 2015 and March 2016 only. The occurrence of shoals with unequal sex ratios during the spawning season has been recorded for several fishes (Morgan and Trippel 1996; Boudinar et al. 2016; Freitas et al. 2018). For fishes that form aggregations during spawning, sex ratio may be highly space-time variable due to spatial segregation by sex during spawning (Macchi et al. 2002) and gender differential movement into and out of the spawning sites, as observed for commercially important Atlantic cod (Morgan and Trippel 1996), Black drum (Macchi et al. 2002) and groupers (Freitas et al. 2018). However, several factors including differential longevity, mortality and catchability may also contribute to the observed gender differences (Hixon et al. 2014; Boudinar et al. 2016; Freitas et al. 2018). Little information is available on the reproduction of ephippids (Hayse 1990; Ditty et al. 1994; the present study) and further research is needed to address this.

Sexual growth dimorphism was not evident in length-mass relationships and the overall length-frequency distributions. The adult males and females demonstrated negative allometric growth because they grew slightly faster in length than in weight. There were no statistical differences in the mass-length relationships between sexes. Negative allometric growth was noted in previous work on *C. faber* (mean TL= 147 mm; $b = 2.75$) in southeastern Brazil (Dias et al. 2014). In the present study, however, the indeterminate individuals showed positive allometric growth because they grew slightly faster in weight than in length. This has been observed in smaller *C. faber* (mean TL= 25 mm; $b = 3.66$) from northern Brazil (Ferraz and Giarrizzo 2015). A size-dependent shift from early allometric positive growth to allometric negative growth may be a necessary step in the development of *C. faber* that will ultimately occupy a pelagic environment (Barros et al. 2015).

The otolith edge-type and RMD analyses showed an annual pattern in the deposition of opaque bands. The lowest RMD and the > 50% proportions of opaque otoliths edges from September 2015 to January 2016, appear to be related to the period of rising water temperature in the study area (Soeth et al. 2015). In *C. faber* from North Atlantic Ocean, the opaque zone deposition in otoliths occurs from winter (January) to early summer (July) (Davis et al. 2015). Slight differences in the deposition period may be related to different age groups analyzed (Hyndes et al. 1992) and environmental factors, such as seawater temperature and variable feeding conditions (Geffen and Nash 1995; Pilling et al. 2007). The results of the present study show that spring and autumn appear to be a primary periods for the deposition of opaque and translucent zones in the otoliths of *C. faber* in subtropical environments.

The results presented in this study showed that small differences in the dataset can strongly influence the model of best fit in fish growth studies. The inclusion of small fish in the dataset favored the VBGF based on AICc selection mainly due to the lack of fit from the both S-Shaped GM and LM that were less accurate for description of *C. faber* at all life stages. The GM and LM models underestimated the maximum asymptotic TL which, in turn, increased the relative growth rate estimates. Although the GM appeared less appropriate for describing male growth, the parameters were obtained by sufficient model support for both sexes ($\Delta i < 2$). The estimated inflection point from the Gompertz model for males (ti = 1.83 years old) and females (ti = 1.96 years old) was close to A_{95} (males A_{95} = 1.79 years old; female A_{95} = 2.29 years old). The inflection point in sigmoid functions can be biologically interpreted as a shift where growth stops increasing and begins to decrease (Thorson and Simpfendorfer 2009). This finding suggests some trade-off between growth and reproduction in *C. faber*, which appears to increase the proportion of energy allocated to reproduction in the post-maturation life stage (Roff 1983). However, changes in somatic growth can also occur as juveniles that emigrate from estuarine nursery grounds to continental shelf habitats (Secor 1999; King 2007; Daros et al. 2012).

The VBGF parameters obtained from the pooled dataset (L_∞ = 508 mm TL, k = 0.22 year^{-1} , t_0 = -0.05 year) were similar to those reported previously for *C. faber* from South Carolina (Hayse 1990: L_∞ = 490 mm TL, k = 0.34 years^{-1}, t_0 = 0.18 year) where seawater surface temperatures range from 8°C to 30°C in the central coast (Calder 1990). Direct comparisons among studies are difficult because differences in the sampling environment and datasets can strongly influence the model parameters (Thorson and Simpfendorfer 2009). In all datasets in the present study, k was smaller than that reported from the South Carolina

study where the oldest fish was 8 years old and the age-0 group represented more than 50 % of the total sample modeled (Hayse 1990). In the present study, the oldest observed fish was 17 years old and age groups between 8 and 11 years old were well represented in the samples. These age-class differences are probably the main reason for the difference in k between studies due to the inverse relationship between L_∞ and k. The inclusion of small individuals into the dataset produced more realistic t_0 estimates (t_0 = -0.05), which in turn modified k and L_∞.

The maximum age recorded for *C. faber* in the present study was two times higher than previously reported from the North Atlantic (Hayse 1990). Large specimens of *C. faber* are common in United States waters (Bell 2005), where the world record specimen of 6,750 g was caught in Chesapeake Bay, Virginia (IGFA 2017). Thus, the observed age differences between studies could be explained by the low number of individuals that were larger than 450 mm TL and also the age estimation method which counted annual increments from whole otoliths (Hayse 1990). Counting whole otoliths tends to underestimate fish age due to the stacking of rings on the otolith edge (Hyndes et al. 1992). However, it is difficult to confirm the main reason for the observed latitudinal age differences as environmental and ecological factors play a role in longevity variation at both intraspecific and intrapopulation levels (Pauly 1980; Secor 1999). Genetic and environmental factors like temperature and salinity can strongly influence fish growth and longevity (Pauly 1980; Boeuf and Payan 2001; Yamahira and Conover 2002). Additionally, human exploitation rates can have a direct impact on the age and size structure of fish populations (Aschenbrenner et al. 2017).

The total length of *C. faber* showed a large variation within age groups which indicates wide variation in individual growth rates. Intrapopulation variability in the growth rates could be explained by genetic, ecological and environmental factors such as discontinuous polymorphisms involving growth rate in discrete populations (Nordeng 1983; Secor 1999), density-dependent intraspecific competition (Hamrin and Persson 1986), habitat quality (Schwartzkopf and Cowan Jr 2017) and other factors including behavior, function and performance (Jørgensen et al. 2016). In addition, large size-at-age variation is common in fishes which employ a multiple batch-spawn strategy (Lowerre-Barbieri et al. 1998), by means of the match or mismatch between the repoduction time (i.e., birth months) and optimal conditions to juvenile fish growth, such as seawater temperature and food availability (Olson 1996; Lowerre-Barbieri et al. 1998, 2011). Such ecological trends could later drive divergent migration behavior or habitat use that also affect individual fish growth (Olson 1996; Secor 1999).

The *C. faber* population under analysis showed a protracted spawning period as reproductive active individuals were identified in samples from October 2015 to January 2016. This period coincides with rising seawater temperatures in the study area (Soeth et al. 2015). The relationship between spawning period and temperature is in agreement with research from the North Atlantic and the Gulf of Mexico which showed that *C. faber* spawns from mid-spring to summer (Hayse 1990; Ditty et al. 1994). In southern Brazil, reproduction peaks through spring and summer have been identified in several fish families, such as Gerreidae (Chaves and Otto 1998), Balistidae (Bernardes and Dias 2000), Tetraodontidae (Rocha et al. 2002), and Sciaenidae (Haluch et al. 2010). This period appears to be linked with favourable conditions for gonadal and initial fish development in estuarine and coastal habitats (Godefroid et al. 1999; Castro et al. 2005; Lowerre-Barbieri et al. 2011; Souza-conceição et al. 2013).

The histological examination of gonadal structure demonstrated that *C. faber* females sustained a constant reserve of primary growth oocytes during all sexual development phases. The presence of pre-vitellogenic and vitellogenic follicles at different development stages, in combination with the presence of postovulatory follicles (POFs), confirmed that *C. faber* is a batch spawner (Hayse 1990; Brown-Peterson et al. 2011). Postovulatory follicles were often recorded in the ovaries of spawning capable and actively spawning *C. faber* females which suggests a high frequency of spawning events across the primary reproductive period (Hunter et al. 1986; Ganias et al. 2007; Brown-Peterson et al. 2011). This protracted spawning period in conjunction with a high frequency of spawns would have a selective advantage, decreasing density-dependent intraspecific competition and increasing the likelihood that larvae or juveniles will find favorable conditions for growth (Johannes 1978; Lowerre-Barbieri et al. 1998).

The most actively spawning females were collected in the southern channel of the PEC, in December. In these individuals, several indicators of the imminent release of gametes (Brown-Peterson et al. 2011) were seen including oocyte hydration and newly collapsed POFs. Moreover, male samples from the same area showed spermiation during macroscopic observations of milt release. These findings suggest that the southern channel of the PEC could be a spawning site for this *C. faber* population. Since the sampling effort was conducted for a full year at this site, and the highest number of larger individuals were collected between October 2015 and December 2015, the data suggest that *C. faber* may display a seasonal movement for spawning aggregation purposes, an event well known to occur in many fish species (Macchi et al. 2002; Sadovy de Mitcheson and Colin 2012; Bueno et al. 2016). These

observations are in agreement with observations drawn from the landings *C. faber* in the artisanal fisheries of SE-S Brazil because of catch associated with large estuary systems increases by over 1,100 % from August to December annually (PMAP-BS 2017a, 2017b). This spawning aggregation behavior could increase the level of local recruitment and further benefit demersal plant-mimetic juveniles through settlement in estuarine regions where they are abundant (Sadovy de Mitcheson and Colin 2012; Barros et al. 2013; Possato et al. 2016). In addition, the timing and location of fish spawning aggregations and variations in local recruitment is a function of different biological (e.g., pelagic larval duration and larval swimming) and physical (e.g., sea currents, coastline and bathymetric variability) processes and interactions (Siegel et al. 2008). To our knowledge, only two studies, that used underwater observations, have reported reproductive aggregations of *C. faber* from the entrance of Sapelo Sound, Georgia State, United States (Chapman 1978) and at the Belize Barrier Reef (Heyman and Kjerve 2008). Some speculation has been made about the potential for spawning aggregations of other Ephippidae, *Platax spp.* from the Republic of Palau, but this hypothesis has not confirmed (Domeier and Colin 1997). Regarding the early life stages of *C. faber*, few studies have reported spatial and temporal distributions. However, most studies that have collected *C. faber* eggs and larvae have done so inside or at the entrance to bays and estuarine systems (Barletta-Bergan et al. 2002; Joyeux et al. 2004; Castro et al. 2005; Bonecker et al. 2009; Burghart et al. 2014), or in coastal waters and riverine frontal areas (Ditty et al. 1994). Although the data available are too limited to make conclusions on *C. faber* reproductive sites, the present study and all previous work suggests that *C. faber* spawning is associated with estuarine systems and costal bays. In addition, mixed schools of spawning capable and regressing *C. faber* females were collected from a shallow rocky reef (<15 meters depth) and an artificial reef (<27 meters depth) on 24 January 2016 and on 31 March 2016 in the present study. Although these individuals did not show oocyte hydration, the GSI values ranged from 0.9 to 8.4 in the presence of POFs. This suggests that, even at low percentages, some *C. faber* individuals may spawn for longer in coastal areas adjacent to the PEC until April.

The present study was in agreement with previous work from subtropical areas of the North Atlantic which showed that males reached maturity at a shorter length and younger age than females (Hayse 1990). While more than 50 % and 100 % (upper A_{95} C.I.) of males are mature by their first and second birthdates, respectively, females spend approximately 0.5 more years than males to reach 50 % and 100 % maturity. These findings suggest that females would be capable of spawning just prior their second birthdate (second spring-summer) and

would be 100 % mature just prior to their third birthdate. Thus, the catch of individuals under 250 mm TL must be restricted to ensure that all individuals have an opportunity to spawn at least once in their lifetime to guarantee stock replenishment.

This study demonstrated that *C. faber* shows early maturation with a life span of more than 15 years in the SW Atlantic Ocean. The observed trade-off between growth and reproduction, elevate GSI values, and an extended spawning season suggests that *C. faber* exhibits a high reproductive capacity in subtropical latitudes. *Chaetodipterus faber* may aggregate seasonally to facilitate spawning thereby increasing the susceptibility of the species to overexploitation (Macchi et al. 2002; Sadovy de Mitcheson et al. 2008). Fishery closures during the spawning season (van Overzee and Rijnsdorp 2014) should be used as a tool to manage the *C. faber* stock in southern Brazil. However, the effects of current harvest levels are unknown and require further study. The location of the main spawning/nursery areas and knowledge of the population dynamics are also necessary to fulfill the prerequisites for informed management of this important fisheries resource.

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CAPÍTULO 3

Stock structure of the Atlantic Spadefish *Chaetodipterus faber* from Southwest Atlantic Ocean inferred from otolith elemental and shape signatures

Stock structure of Atlantic Spadefish *Chaetodipterus faber* from Southwest Atlantic Ocean inferred from otolith elemental and shape signatures

Marcelo Soeth, Henry Louis Spach, Felippe Alexandre Daros, Johnatas Adelir-Alves, Ana Claudia Oliveria de Almeida, Alberto Teodorico Correia

ABSTRACT

The Atlantic spadefish, *Chaetodipterus faber,* is an economically important species along the Southwest Atlantic Ocean, especially in the southeastern-south Brazil. Despite this, knowledge about stock structure is scarce and, at present, is currently no formal management strategy to ensure the long-term sustainability of the *C. faber* fishery in Brazil. In order to understand the stock structure of *C. faber* in the Southwest Atlantic, a total of 100 individuals ranging from 30 to 40 cm total length were collected from the five main fishery regions of Brazil [Espírito Santo (ES), Rio de Janeiro (RJ), São Paulo (SP), Paraná (PR), and Santa Catarina (SC)], between December 2015 and March 2016. The shape outline of each otolith was assessed using Elliptic Fourier descriptors (EFD). Multi-Elemental signatures (MES) of whole otoliths were obtained using inductively coupled plasma mass spectrometry. Data were analyzed through uni- and multivariate statistics. Canonical analysis of principal coordinates indicated that spatial differences were mainly driven by Sr/Ca ratios, Ba/Ca ratios and EFD 14. Combining data from both techniques (EFD and MES), the leave-one-out classification re-assigned individuals to their region of origin with an accuracy of 100% (ES), 85% (RJ), 80% (SP), 85% (PR), and 65% (SC). The hereby results indicate that the connectivity between the local population of *C. faber* in the ES region (20°S) with the southern populations (>22°S) is limited; moreover, data suggest the presence of spatially structured semi-discrete groups between 23°S and 27°S. Despite the possibility of intermixing *C. faber* populations in the Brazilian Southwest Atlantic coast, local populations should be regarded as different stocks for fisheries management purposes. However, at present, the degree of intermixing and the contribution that each local population receive from distant recruitment sources is unknown and demands further studies.

Keywords

Ephippidae; Stock identification; Brazilian coast; Otolith phenotype;

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1. **Introduction**

The Atlantic spadefish, *Chaetodipterus faber,* is a reef-associated fish found in the coastal ecosystems of the Western Atlantic Ocean from Massachusetts (USA) to southern Brazil, including the Caribbean Sea and Gulf of Mexico (Burgess, 2002; Machado et al., 2017). Demersal early juveniles are common in estuaries and coastal regions (Barros et al., 2013; Soeth et al., 2014), while adults of *C. faber* are benthopelagic and frequently observed in reef environments of the continental shelf up to a depth of 40 meters (Godoy, 2002; Luiz et al., 2008). In the past decade, the artisanal *C. faber* fishery landed approximately 260 tons per year along the Brazilian coast, of which 80% was from the subtropical region (IBAMA, 2009; MPA, 2012) where *C. faber* is particularly important to artisanal fisheries operating in coastal areas (PMAP-BS, 2017a, 2017b). Furthermore, the annual average landings for industrial *C. faber* fisheries increased by 6 times, rising from 36 to 240 tons from 2000 to 2017 (UNIVALI/CTTMar, 2010, 2013a, 2013b, PMAP-SC, 2018). However, at present, there is no specific legislation to ensure the long-term sustainability of the *C. faber* fishery in Brazil.

Rational and sustainable management requires a proper understanding of the structure of the fishery's stock (Begg et al., 1999; Begg and Waldman, 1999; Secor, 2013). The term "stock" corresponds to an intra-specific semi-discrete group of randomly mating individuals that show temporal or spatial integrity (Ihssen et al., 1981), with some definable attributes of interest to managers (Begg et al., 1999). Several techniques based on phenotypic and genetic variation have been successfully employed for stock identification and delineation, including morphological analyses, comparison of life-history traits, otolith shape and elemental analyses, and genetic markers (Begg and Waldman, 1999; Secor, 2013). Recently, it has been shown, using mitochondrial DNA, that *C. faber* exhibits spatial structure between tropical (<20°S) and subtropical (from 23°S to 27°S) regions along the Brazilian coast (Machado et al., 2017), which suggests the presence of two allopatric groups in this region.

However genetic data provide a rather conservative measure of population differentiation as low levels of genetic mixing is, generally, sufficient to obscure the results (Lowe and Allendorf, 2010; Reiss et al., 2009). Therefore, other phenotypic attributes and criteria may also be used for stock discrimination and management of fisheries (Begg et al., 1999; Correia et al., 2012; Secor, 2013). The chemical composition and shape of otoliths are powerful tools in solving population structure problems of fishes (Callicó Fortunato et al., 2017; Campana and Casselman, 1993; Correia et al., 2011; Moreira et al., 2018). Otolith phenotypic variation assists in distinguishing between groups of fish that have experienced

prolonged separation of post-larval stages in partially independent environmental (e.g., water temperature, salinity and feeding conditions) regimes (Begg et al., 1999; Cardinale et al., 2004; Correia et al., 2014; Kritzer and Sale, 2004). Phenotypic variation may even occur in the absence of genetic differences or in addition to the genetic component that may act synergistically with phenotypic-induced otolith characters (Berg et al., 2018; Cardinale et al., 2004; Correia et al., 2012; Gillanders et al., 2011). As such, otolith phenotypic tools have been successfully applied in stock discrimination purposes (Begg and Waldman, 1999; Correia et al., 2011; Secor, 2013). Otoliths are considered to be metabolically inert structures that grow continuously throughout the fish's life, recording the aquatic environment where fish lived (Campana et al., 2000; Campana and Neilson, 1985; Hamer et al., 2006). Although the incorporation of different elements in the aragonite matrix of otoliths is still a poorly understood process, some elements, such as strontium and barium, display high correlations between environmental and otolith concentration (Albuquerque et al., 2010; Bath et al., 2000; Webb et al., 2012). Otolith shape is species-specific and may also shows intra-specific geographic variation in relation to environmental factors and fish growth (Campana and Neilson, 1985; Libungan et al., 2015; Mosegaard et al., 1988). While environment essentially alters the otolith growth rate, which in turn modifies otolith shape, genetically induced changes could locally alter otolith shape (Berg et al., 2018; Cardinale et al., 2004; Mosegaard et al., 1988). The extent to which otolith shape differences are genetically or environmentally induced remains unclear (Cardinale et al., 2004), but otolith shape analysis has been successfully used to discriminate among fish stocks (Campana and Casselman, 1993; Ferguson et al., 2011; Libungan et al., 2015). Furthermore, a cumulative and comparative framework may maximize the likelihood of correctly delineating stocks using fish otoliths (Begg and Waldman, 1999; Callicó Fortunato et al., 2017; Ferguson et al., 2011; Longmore et al., 2010). Moreover, these complementary methods could help us to unravel the stock structure of *C. faber* in a possible high gene flow region (Machado et al., 2017), but with known oceanographic environmental heterogeneity (Castro et al., 2006; Castro and Miranda, 1998; Piola et al., 2000).

In the present work, otolith elemental and shape signatures were used as an alternative approach toward the delineation of the structure of the *C. faber* stocks in the main fishery areas of the Southwestern Atlantic Ocean. Ultimately, the study intention was to determine whether distinct otolith natural tags occur for adult fish captured in the different fishery regions and thereby suggesting that they may represent discrete local populations.

2. Materials and Methods

2.1. Study area

The study area encompasses the region of the tropical and subtropical Southwest Atlantic Ocean, which includes the southeastern-south Brazilian coast from the state of Espírito Santo (ES, 20ºS) to the state of Santa Catarina (SC, 27ºS; Fig. 1). The continental shelf includes different physical and biogeochemical environments, namely the southern part of the Abrolhos-Campos Region (ACR, 15ºS - 23ºS) and the South Brazil Bight (SBB, 23ºS - 28ºS) (Castro and Miranda, 1998). In these regions, a latitudinal thermal and salinity gradient is present (Piola et al., 2000). The Brazil Current (BC) transports the warm and salty Tropical Water (TW; temperature > 20ºC; salinity > 36) southwestward within the mixed layer (0-200 m) on the continental slope (Castro et al., 2006; Silveira et al., 1994). At thermocline depths, BC transports the South Atlantic Central Water (SACW; temperature between 6ºC and 20ºC >; salinity between 34.5 and 36) (Castro et al., 2006; Piola et al., 2000; Silveira et al., 1994). The cool and less saline Coastal Water (CW), occupying the inner and medium shelf, is formed primarily from river runoff water, estuarine plumes, SACW, and TW (Castro et al., 2006; Castro and Miranda, 1998). Wind-driven coastal upwelling of SACW in large portions of the ACR and SSB shelf, especially during the austral summer along narrow continental shelf regions between 20ºS - 23ºS and 28ºS - 29ºS (Fig. 1) (Castro et al., 2006; Emílsson, 1961; Palóczy et al., 2016; Rodrigues and Lorenzzetti, 2001).

2.2. Fish sampling

Fish sampling took place between December 2015 and March 2016. A total of 214 individuals were collected by spearfishing or obtained from artisanal fishermen using gill nets in coastal areas of Espírito Santo (ES), Rio de Janeiro (RJ), São Paulo (SP), Paraná (PR), and Santa Catarina (SC). Upon collection or immediately after landing, fish were preserved on ice then processed in the laboratory. The individuals were measured for total length (TL, 1 mm), and weighed (W, 1 mg). Sagittal otoliths were removed using plastic forceps to avoid metallic contamination, cleaned of adherent tissues with ultrapure water (Milli-Q water), dried with lint-free paper, and stored dry in labeled Eppendorf tubes. To minimize the ontogenetic effects on phenotypic variation (Campana et al., 2000), the size range of the individuals selected for otolith shape and elemental analyses was restricted to 30 - 40 cm TL (Table I).

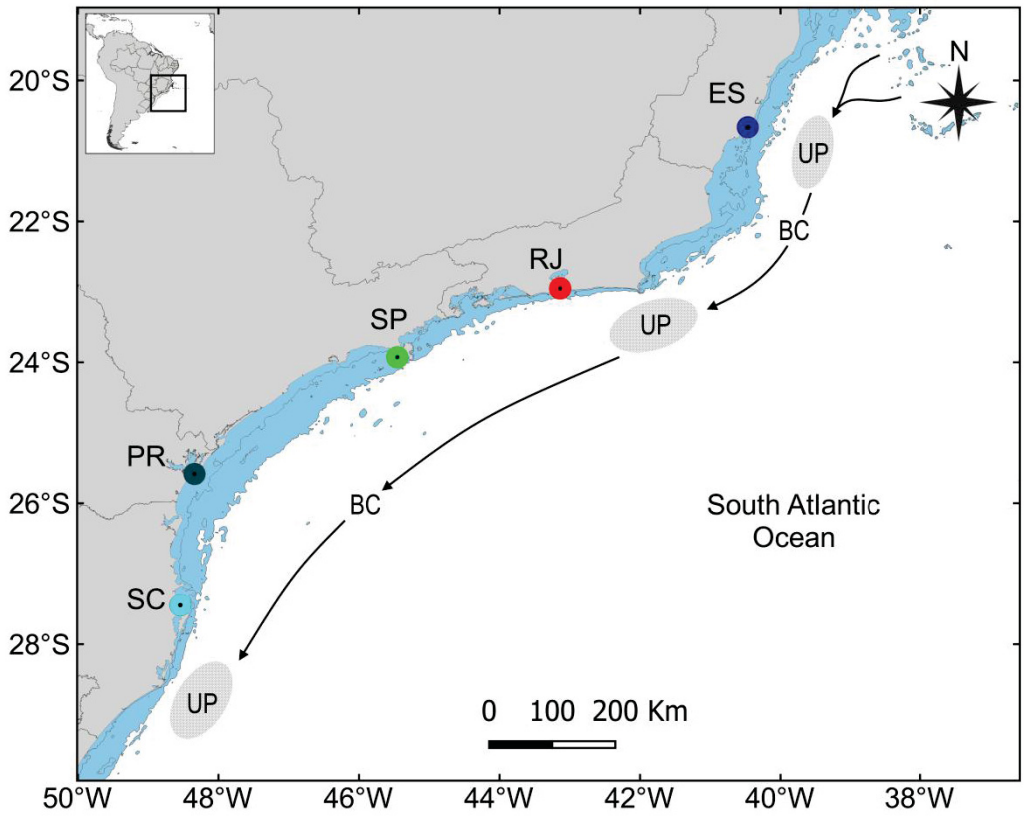

Fig. 1. Map indicating sampling regions [Espírito Santo (ES), Rio de Janeiro (RJ), São Paulo (SP), Paraná (PR), and Santa Catarina (SC)] of *Chaetodipterus faber* in SW Atlantic, SE-S Brazil. Bathymetric contours of 20 and 50 m depth are shown as blue. Dark lines and arrows represent the Brazil Current (BC). The main coastal upwelling regions (UP) are also indicated.

Table I. Sampling region, sampling period, sample size (n), mean total length (TL) and mean otolith mass (OM) by sampling region. Espírito Santo (ES); Rio de Janeiro (RJ); São Paulo (SP); Paraná (PR); Santa Catarina (SC). Mean values ± standard deviation.

Sampling region	Sampling period	n	TL (mm)	OM (mg)
ES - 20°3'S, 40°2W	March 2016	20	343 ± 13	36 ± 9
RJ - 23°0'S, 43°8'W	January 2016	20	325 ± 15	28 ± 4
SP - 23°5'S, 45°3'W	January 2016	20	323 ± 24	25 ± 5
PR - 25°3'S, 48°2'W	December 2015	20	373 ± 24	33 ± 5
SC - 27°2'S, 48°3'W	December 2015	20	318 ± 15	26 ± 4

2.3. Otolith shape analysis

Unbroken right otoliths were placed with the sulcus acusticus up and the rostrum to the left. Orthogonal two-dimensional digital images of otoliths were captured under a stereomicroscope (x10 magnification) coupled to a camera (Olympus, SC30). Full color (*.jpg), and high resolution (2048 x 1532) microphotographs were captured using reflected light against a dark background using the Olympus Image Analysis 5.0 software.

The shape outline of each otolith was assessed with Elliptic Fourier analysis. For this, digitalized otolith images were read using the shapeR package (Libungan and Pálsson, 2015) within the R programming environment (R Development Core Team, 2017). The outlines were detected by first transforming the images into gray-scale and then converting them to B&W images using a threshold pixel value. The extracted outlines of each otolith were checked to see if the outline matched the original image (Fig. 2A). To eliminate pixel noise from the captured outline, a weighted moving average over three successive coordinate points was used (Libungan and Pálsson, 2015). The Elliptic Fourier descriptors (EFD) were made invariant with respect to the starting point, scale, rotation and fish size. As a consequence of the normalization process the first three descriptors are omitted (Libungan and Pálsson, 2015). Descriptors that showed a significant interaction between TL and region were excluded (i.e., seven descriptors) from further analysis (Libungan et al., 2015; Longmore et al., 2010). Thus, 38 (48−3-7=38) normalized EFD remained for the subsequent analyses.

2.4. Otolith elemental analyses

Right otoliths were cleaned and decontaminated following standard protocols (Rooker et al., 2001). Decontaminated otoliths were weighed (0.0001 g) and dissolved for 15 min in 1 mL of ultrapure HNO_3 (Fluka TraceSelect) and then diluted with Milli-Q-Water to a final volume of 10 mL (Correia et al., 2011). Blank and otolith certificated material vials were similarly prepared for blank corrections and accuracy calculation. All solutions were further diluted in the lab [HNO_3 2% (v/v) and TDS < 0.2%] prior to chemical analyses. Otolith elemental composition of whole otoliths was determined using a double focusing magnetic sector field instrument ICP-SF-MS (Thermo ICP-MS x series, Thermo Electron Corporation). False readings from spectral interferences were avoided by performing all measurements at a medium resolution setting ($m/\Delta m=4000$). The ICP-SF-MS was equipped with a micro-flow nebulizer (PFAAR35-1-C1E, Glass Expansion), operated in the self-aspirating mode (sample

uptake rate ~0.93 L min^{-1}). To minimize the effect of any plasma fluctuations or different nebulizer aspiration rates among samples, ^{115}In was added at a set concentration to all samples and standards as an internal standard.

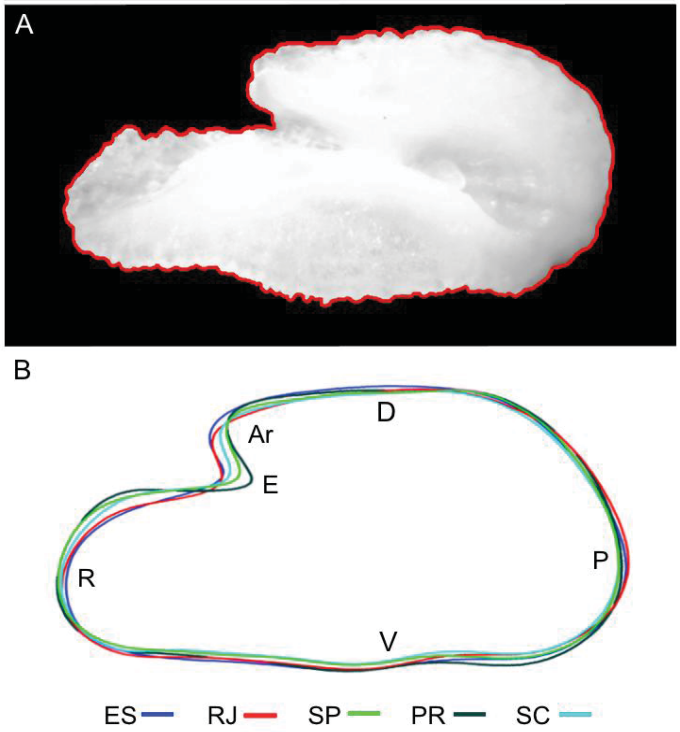

Fig. 2. Digital image of the medial face of the right sagittal otolith of *Chaetodipterus faber* showing the extracted outline (A). Mean otolith shape based on Elliptic Fourier descriptor reconstructions for *Chaetodipterus faber* from Espírito Santo (ES), Rio de Janeiro (RJ), São Paulo (SP), Paraná (PR), and Santa Catarina (SC) Image codes: dorsal (D), ventral (V), post-rostrum (P), excisura major (E), rostrum (R) and anti-rostrum (Ar).

After a preliminary analysis, six elements (^{44}Ca, ^{88}Sr, ^{137}Ba, ^{26}Mg, ^{55}Mn, and ^{66}Zn), widely used for fisheries discrimination purposes (Correia et al., 2011; Ferguson et al., 2011; Moreira et al., 2018) and already reported in southern Brazilian fishes (Avigliano et al., 2017; Daros et al., 2016a), were identified as useful biogeochemical tags, being consistently detectable in whole otoliths by inductively coupled plasma mass spectrometry (ICP-MS-SB). Analytical accuracy was determined using a multi-elemental certified otolith material (FEBS-1) with a value of recovery obtained ranging between 81% and 114 %. The precision of replicate analyses of individual elements ranged between 2% and 5% of the relative standard deviation (RSD). The limits of detection were calculated from the individual calibration

curves using the three sigma criteria and were (in μgL^{-1}): ^{44}Ca (10000), ^{88}Sr (1000), ^{26}Mg (20), ^{66}Zn (10), ^{55}Mn (2), and ^{137}Ba (1). Concentrations of trace elements, originally in µg element L^{-1} solution, were transformed to µg element g^{-1} otolith and then to µg element g^{-1} calcium.

2.5. Data analysis

The average EFD reconstruction of the otolith shapes was used to visually evaluate the main differences in otolith contours among regions (Libungan and Pálsson, 2015). Elemental signatures were checked for normality and homogeneity of variance prior to statistical analysis. These assumptions were not met after log(x+1) transformation to all elements. Therefore, differences in single elements were analyzed by permutational univariate analysis of variance (PERANOVA), while permutational multivariate analysis of variance (PERMANOVA) was used to compare multi-elemental signatures (MES) and EFD among regions (Avigliano et al., 2017b; Ferguson et al., 2011; Fowler et al., 2015). For multivariate and univariate analyses, dissimilarity matrices were based on Euclidean distance, and *p*-values were generated using 9999 permutations. Models found to be statistically significant were followed by permutational pairwise comparisons (pseudo-*t* statistic) among all pairs of levels (Anderson et al., 2008). The canonical analysis of principal coordinates (CAP) was used to visualize spatial differences and to examine the re-classification accuracy (leave-one-out diagnostic) of matching each individual fish with its original location (Anderson and Willis, 2003). Additionally, as CAP analyses were based on Euclidean distance, a "trace" test statistic was provided, which is equivalent to multivariate analysis of variance (Anderson et al., 2008). Pearson correlations ($r > 0.50$) of the original variables with canonical axis patterns were shown graphically. To ensure that differences in otolith mass among regions did not confound any site-specific differences in otolith chemistry, the relationship between elemental/Ca ratios and otolith mass (OM) was evaluated using analysis of covariance (ANCOVA) with OM as a covariate (Campana et al., 2000; Daros et al., 2016a). This relationship was significant for Sr/Ca (positive relationship, $r^2 = 0.33$, $p < 0.05$) and for Zn/Ca (negative relationship, $r^2 = 0.27$, $p < 0.05$). Both relationships were successfully removed by means of subtraction of the common within-group linear slope multiplied by the OM from the observed element/Ca ratios. All uni- and multivariate analyses were performed using the lawstat and stats packages within the R programming environment (R Development Core Team, 2017) and PRIMER 7 v.7.0.13 software.

3. Results

3.1. Otolith shape analysis

The otolith shape reconstruction from the EFD averages demonstrated, visually, distinct differences among regions, especially in the excisura, rostrum, and antirostrum (Fig. 2). The differences in EFD among regions were significant (PERMANOVA, pseudo-F = 2.5726; df = 4, 95; $p < 0.01$). PERMANOVA pairwise comparisons detected EFD differences (pseudo-t test, $p < 0.05$) between PR and RJ, PR and SC, PR and SP, RJ and SP. The PERMANOVA results were in agreement with the CAP (*trace* CAP *statistic* = 2.46; $p < 0.001$). Vector overlays indicated that group separation on CAP Axis 1 ($\delta_1^2 = 0.77$) was primarily driven by EFD 17 (Pearson, r = -0.55) and EFD 14 (Pearson, r = 0.53) while on CAP Axis 2 ($\delta_1^2 = 0.63$) was primarily influenced by EFD 8 (Pearson, r = -0.50). PR and SC demonstrated a minor data overlap in CAP, and were clearly different from RJ; RJ and ES also displayed a relatively high degree of overlap. SP showed major data overlapping among groups (Fig. 3A). The leave-one-out classification assigned individual fish to their collection regions with an accuracy ranging from 50% (ES) to 65% (SC) and an overall re-classification success of 59% (Table II).

3.2. Otolith microchemical signatures

3.2.1. Single elemental analysis

All element/Ca ratios for the otoliths differed among regions (PERANOVA; $p < 0.05$) with the exception of Mg/Ca ratios (Fig 4; Table III). Region explained the most of the variation in Sr/Ca, Mn/Ca, and Ba/Ca ratios (Table III). The Sr/Ca ratios across regions ranged from 5,680 μg g^{-1} to 12,465 μg g^{-1}. The Sr/Ca ratios from ES otoliths was higher (pseudo-t test, $p < 0.05$) in comparison with other regions, while SP and PR otoliths presented the lowest Sr/Ca ratios (pseudo-t test, $p < 0.05$; Fig. 4A). The Ba/Ca ratios across regions ranged between 2.9 and 43.7 μg g^{-1}. The Ba/Ca ratios from RJ, SP and SC otoliths were significantly lower in comparison with ES and PR otoliths (pseudo-t test, $p < 0.05$; Fig. 4B). The range of Mn/Ca ratios across regions was 1.3 to 27.0 μg g^{-1}. Otoliths from ES demonstrated extremely low Mn/Ca ratios when compared to the other regions (pseudo-t test, $p < 0.05$; Fig. 4C). The Mg/Ca ratios across regions varied between 13.3 and 123.1 μg g^{-1}; no

statistically significant differences were found (PERANOVA, $p > 0.05$; Fig. 4D). The range of Zn/Ca ratios across regions was 27.3-182.9 µg g^{-1}. The Zn/Ca ratio from ES otoliths was significantly higher (pseudo-*t* test, $p < 0.05$) in comparison with RJ and SC (Fig. 4E).

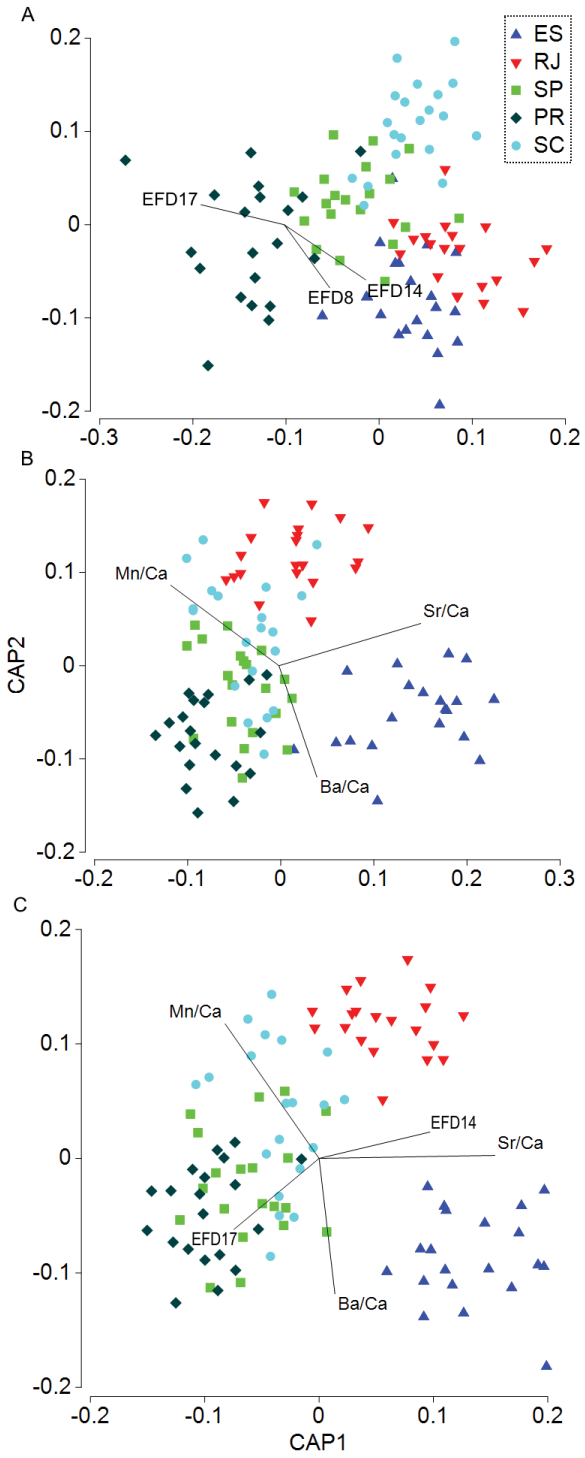

Fig 3. Canonical Analysis of Principal Coordinates (CAP) based on the Elliptic Fourier descriptors (A), Multi-elemental signatures (B), and combining techniques (C) for

Chaetodipterus faber from five sampling regions [Espírito Santo (ES), Rio de Janeiro (RJ), São Paulo (SP), Paraná (PR), and Santa Catarina (SC)].

Table II. The leave-one-out re-classification matrix of *Chaetodipterus faber* based in the Elliptic Fourier descriptors (EFD), Multi-elemental signatures (MES), and combined techniques (EFD + MES).

EFD	Predicted region					%correct	%overall
Original group	ES	RJ	SP	PR	SC	re-allocation	re-allocation
ES	**10**	4	3	0	3	50	
RJ	4	**11**	4	0	1	55	
SP	1	3	**13**	0	3	65	59
PR	3	0	2	**12**	3	60	
SC	0	3	4	0	**13**	65	
MES	Predicted region					%correct	%overall
Original group	ES	RJ	SP	PR	SC	re-allocation	re-allocation
ES	**18**	0	2	0	0	90	
RJ	0	**17**	0	0	3	85	
SP	0	0	**12**	3	5	60	76
PR	0	0	2	**18**	0	90	
SC	0	3	4	2	**11**	55	
EFD + MES	Predicted region					%correct	%overall
Original group	ES	RJ	SP	PR	SC	re-allocation	re-allocation
ES	**20**	0	0	0	0	100	
RJ	0	**17**	1	0	2	85	
SP	0	0	**16**	2	2	80	83
PR	0	0	3	**17**	0	85	
SC	0	2	4	1	**13**	65	

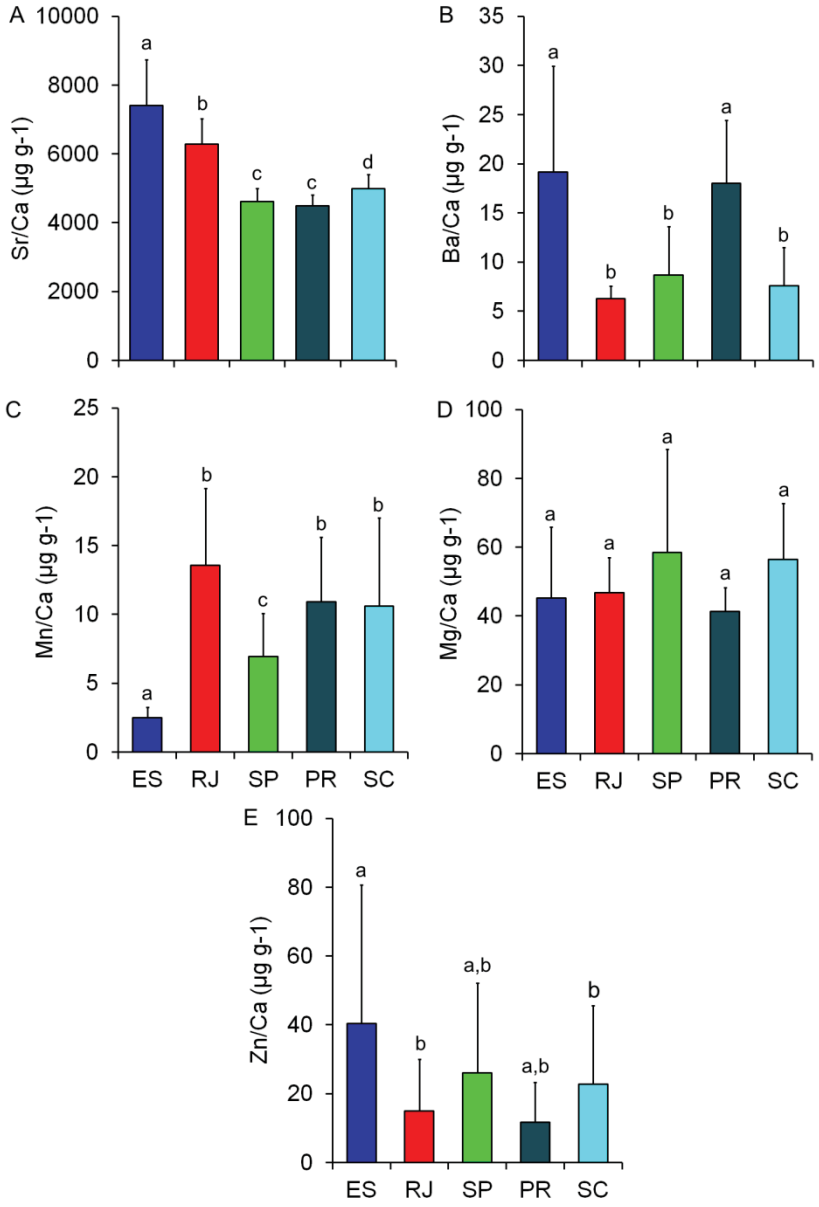

Fig. 4. Regional comparison of element/Ca ratios from the whole otoliths of *Chaetodipterus faber* caught between December 2015 to March 2016 in coastal areas of Espírito Santo (ES), Rio de Janeiro (RJ), São Paulo (SP), Paraná (PR), and Santa Catarina (SC). (A) Sr/Ca ratios. (B) Br/Ca ratios. (C) Mn/Ca ratios. (D) Mg/Ca ratios. (E) Zn/Ca ratios. Different letters above the boxes indicate significant differences (pseudo-*t* test, $p < 0.05$) observed by permutational univariate pair-wise analysis among regions. Mean values ± standard deviation. Detrended values for Sr/Ca and Mn/Ca.

Table III. Regional comparison of element/Ca ratios by permutational univariate analysis of variance from the whole otolith of *Chaetodipterus faber* caught between December 2015 and March 2016 in coastal areas of Espírito Santo, Rio de Janeiro, São Paulo, Paraná, and Santa Catarina, Brazil.

Element	Source	df	MS	pseudo-*F*	*p*	Estimates (%)
Sr/Ca	Region	4	0.168	64.77	0.0001	76.1
	Residual	95	0.003			23.9
	Total	99				
Ba/Ca	Region	4	0.762	24.03	0.0001	53.5
	Residual	95	0.032			46.5
	Total	99				
Mn/Ca	Region	4	1.099	38.27	0.0001	65.1
	Residual	95	0.029			34.9
	Total	99				
Mg/Ca	Region	4	0.058	2.41	0.0554	6.6
	Residual	95	0.024			93.4
	Total	99				
Zn/Ca	Region	4	0.012	3.00	0.0224	9.1
	Residual	95	0.004			90.9
	Total	99				

3.2.2. Multi-elemental analysis

There were significant differences in multi-elemental otolith signatures among regions (PERMANOVA, pseudo-F = 23.015; df = 4, 95; $p < 0.0001$). Multi-elemental otolith signatures were not significant different between SC and SP only (pseudo-t test, $p > 0.05$). The PERMANOVA results were in agreement with the CAP (*trace* CAP *statistic* = 1.75; $p < 0.001$). ES demonstrated a minor data overlap in CAP and is clearly different from the other regions. SP, PR, and SC showed a relatively high degree of overlap. Vector overlays indicated that group separation on CAP Axis 1 ($\delta_1^2 = 0.77$) was primarily driven by Sr/Ca ratios (Pearson, r = 0.92) and Mn/Ca (Pearson, r = -0.70). Separation on CAP Axis 2 ($\delta_1^2 = 0.69$) was primarily driven by Ba/Ca ratios (Pearson, r = -0.74), and Mn/Ca ratios (Pearson, r = 0.49) (Fig. 3B). The leave-one-out re-classification corroborated most of the patterns

observed in the CAP and PERMANOVA analyses where samples from SC and SP showed the highest misclassification error. Individual fish were assigned to their collection regions with an accuracy ranging from 55% (SC) to 90% (both ES and PR), and an overall classification success of 76% (Table II).

3.3. Otolith shape and chemical techniques combined

PERMANOVA showed significant differences among regions using the combined data from MES and EFD (pseudo-F = 3.99; df = 4, 95; $p < 0.0001$). PERMANOVA pairwise comparison detected differences ($p < 0.05$) among all regions. The CAP using the combined data also showed significant differences among regions (*trace* CAP *statistic* = 1.75; $p < 0.001$). ES demonstrated no data overlap in CAP. RJ showed a minor data overlap. SP, PR, and SC were, again, showed a relatively higher degree of overlap. Vector overlays indicated that group separation on CAP Axis 1 ($\delta_1^2 = 0.89$) was primarily driven by Sr/Ca ratios (Pearson, r = 0.89) and EFD 14 (Pearson, r = 0.55). Separation on CAP Axis 2 ($\delta_1^2 = 0.83$) was primarily influenced by Ba/Ca ratios (Pearson, r = 0.69), Mn/Ca ratios (Pearson, r = -0.50; Fig. 3C). Overall re-classification success (leave-one-out) using the combined data was 83%. Individual fish were assigned to their collection regions with an accuracy ranging from 65% (SC) to 100% (ES) (Table II; Fig 5).

4. Discussion

This study examined the regional differences in otolith chemical and shape signatures of *C. faber* individuals collected along the Southwestern Atlantic Brazilian coast. The elemental chemical composition and Elliptical Fourier descriptors of whole otoliths successfully distinguished individuals from the five regions sampled and suggesting that there was more than one local population between 20°S and 27°S in the Southwestern Atlantic. Additionally, results from both methods were consistent with combined results from both methods providing the most accurate stock delineation.

The chemical composition and shape outline of otoliths are the result of processes occurring throughout the fish's life history (Campana, 1999; Campana and Casselman, 1993). The variation in EFD among regions provided a lower overall re-classification accuracy in comparison with MES. However, re-classification success was slightly higher (up to 10%) for SP and SC samples when using EFD variables alone. During early life stages, otolith shapes

are generally more uniform and mainly linked to fish size, indicating an ontogenetically determined development (Capoccioni et al., 2011; Vignon, 2012). In general, after fish reach sexual maturity, otoliths show a more constant pattern in relation to fish size (Capoccioni et al., 2011; Carvalho et al., 2015; Vignon, 2012). In the present study, specimens of *C. faber* were restricted to adults between 30 and 40 cm TL (Hayse, 1990). Thus, the observed *C. faber* otolith shape variation among regions most probably results from the influences of both genetic and environmental factors (Berg et al., 2018; Bose et al., 2017; Waldman, 1999).

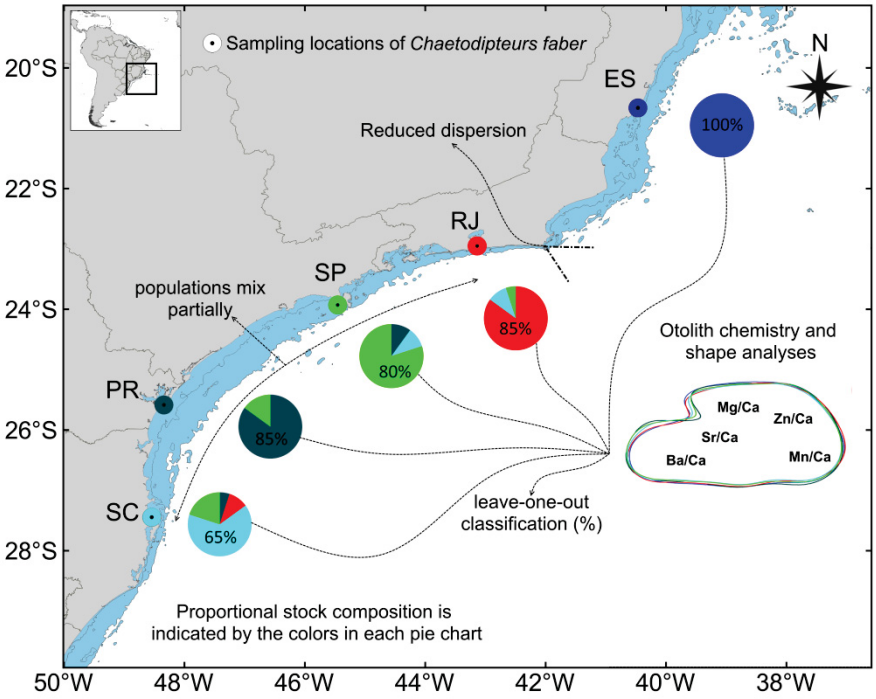

Fig. 5. The leave-one-out analysis of *Chaetodipterus faber* correctly allocated (%) to their respective collection regions based in combined Elliptic Fourier descriptors and Multi-elemental signatures. The proportional stock composition is indicated by the colors in each pie chart. Espírito Santo (ES), Rio de Janeiro (RJ), São Paulo (SP), Paraná (PR), and Santa Catarina (SC).

Factors including temperature, salinity, photoperiod, and feeding regime, have a strong influence on calcium carbonate deposition and consequently on the morphology of otoliths (Campana and Neilson, 1985; Mosegaard et al., 1988; Vignon, 2012). Together with other abiotic factors, latitudinal variations in water temperature could affect fish growth and concurrently driving the structure of reef benthic communities (Aued et al., 2018) that are important feeding environments for *C. faber* (Hayse, 1990). Therefore, because of the

heterogeneous environment of the study area, differences in fish growth conditions could have a major influence on variability in otolith shape in *C. faber* (Campana and Casselman, 1993; Campana and Neilson, 1985; Vignon, 2012).

Otolith shape analysis failed however to distinguish ES samples, even though ES population are known to form an allopatric population distinct from those farther south (Machado et al., 2017). This study was limited by having little information on the contributions of environmental and genetic factors, but the results may also suggest that genetic component (Begg et al., 1999; Berg et al., 2018; Machado et al., 2017) has a reduced influence on *C. faber* otolith shape across sampling regions.

All element/Ca ratios, with the exception of the Mg/Ca ratio, differed among regions, and presented values within the ranges previously reported for other marine fishes in the same geographic area (Avigliano et al., 2017; Callicó Fortunato et al., 2017; Daros et al., 2016). Sr/Ca, Mn/Ca, and Ba/Ca ratios accounted for most of the regional variation. Concentrations of trace elements in otoliths may be influenced by salinity, temperature, diet and physiological factors (Elsdon and Gillanders, 2003; Walther and Thorrold, 2006; Webb et al., 2012), but may also to be under some degree of genetic control (Gillanders et al., 2011). Among element/Ca ratios, Sr/Ca variation was the most consistent among regions and contributed the most to the group separation in CAP analysis. Sr/Ca ratios across sampling regions exhibited a latitudinal trend, with highest values in ES and lowest in SP and PR, as expected according with the seawater surface salinity in coastal areas (Emílsson, 1961; Piola et al., 2000). Ambient water has been reported as the primary contributor of Sr isotopes to otoliths, with a known strong and positive relationship between otolith Sr content and water salinity (Gibson-Reinemer et al., 2009; Walther and Thorrold, 2006; Webb et al., 2012); moreover a lowest positive relationship between otolith Sr content and water temperature has also recorded for some species (Bath et al., 2000; Reis-Santos et al., 2013a). ES samples showed the highest Sr/Ca ratios. These samples were collected on the continental shelf of the Tubarão Bight, which is dominated by the warm saline TW year-round (Castro and Miranda, 1998; Palóczy et al., 2016). Despite the influence of the SACW in the Tubarão Bight (Palóczy et al., 2016), upwelling processes are more intense in the summer and southward (21°S - 23°S), where the Brazilian coast exhibits a sudden change in the orientation of the coastline and water depth (Castro et al., 2006; Castro and Miranda, 1998; Rodrigues and Lorenzzetti, 2001). The lower Sr/Ca ratios were found in SP and PR individuals. This area exhibits an extensive continental shelf (>200 km) and CW salinities tends to decrease due to the lower influence of TW since the Brazil Current flows farther from the shoreline in this area (Emílsson, 1961; Piola et al.,

2000). These results indicate that Sr/Ca ratio can be useful as a potential stock marker for *C. faber* and, probably to other coastal fishes in the Southwest Atlantic.

The highest Ba/Ca ratios found in ES and PR otoliths may be attributed to increased Ba concentrations in the ambient water (Albuquerque et al., 2010; Bath et al., 2000; Webb et al., 2012). High Ba levels in marine environment are associated with (1) terrestrial runoff (Hamer et al., 2006; Moreira et al., 2018; Shaw et al., 1998), (2) upwelling phenomenon (Lea et al., 1989), (3) water contamination/pollution (Gomes et al., 2017), and (4) Ba enrichment in saline environments via advective exchange between an aquifer (groundwater) and the coastal ocean (Shaw et al., 1998). Furthermore, the otolith aragonite matrix can be compromised at high temperatures, so that Ba, and Sr, are more readily incorporated into the otolith at higher temperatures and salinities (Webb et al., 2012). The Ba concentrations in the ES coastal waters may be sustained by different sources, including the medium-sized Paraíba do Sul and Doce rivers, coastal upwelling and likely also the Vitória Eddy, when it reaches the shelf (Ekau and Knoppers, 1999; Gomes et al., 2017; Palóczy et al., 2016). On the other hand, the Ba concentrations in the PR coastal waters may be influenced by the outflows of freshwater from Ribeira do Iguape river and many small-medium size estuaries (e.g., the complex estuary of Paranaguá, Babitonga Bay, and the Cananéia-Iguape estuary) that contribute to the mixing of CW in this region (Daros et al., 2016; Marone et al., 2010). Although the Br/Ca ratios found in ES and PR were statistically equal, it seems that ES and PR could have different sources of Ba or different level combinations of sources.

ES samples presented comparatively low Mn/Ca ratios. This is in agreement with previous studies that suggest that species with higher Sr levels tend to display lower levels of Mn in otoliths (Hamer and Jenkins, 2007). Moreover, while Sr incorporation into otoliths is influenced by water chemistry, Mn appears to be regulated by physiological mechanisms (Elsdon and Gillanders, 2003) and the influence of environmental factors remains unclear (Hamer and Jenkins, 2007). It is known that dissolved Mn is rapidly precipitated in the marine environment and that concentrations are generally several orders of magnitude higher in marine sediments than in seawater (Thomas and Bendell-Young, 1999). It is possible that marine currents induce sediment resuspension in the shallow environments of the South Brazil Bight (SBB), and that the resuspended sediment can become trapped in the rocky reef coverage that makes up the *C. faber* diet (Gordon et al., 2016; Hayse, 1990). Therefore, the differences in Mn/Ca ratios may not necessarily represent differences in water chemistry. Variation in Mn/Ca ratios among regions is more likely to represent heterogeneity in *C. faber*

feeding habitats and in trophic links (Elsdon and Gillanders, 2003; Gibson-Reinemer et al., 2009; Hayse, 1990; Thomas and Bendell-Young, 1999).

ES samples were fully re-classified into a discrete group by combining both techniques. These results indicate that for this region (20°S), connectivity with southern populations (>22°S) is limited, supporting the previous findings of a recent mitochondrial genetic study (Machado et al., 2017). Additionally, the differences among all regions from SBB and the re-classification rates from combined techniques indicate the presence of semi-discrete, spatially structured, phenotypic groups (Ihssen et al., 1981), which suggests prolonged separation of post-larval stages in partially independent environmental regimes (Begg et al., 1999; Kritzer and Sale, 2004). These results also suggest a limited degree of mixing of adult populations among regions from SBB. However, even with low exchange rates of individuals between regions, spatial connectivity scales for adults of *C. faber* in SBB could be very high (up to 700 km). The low re-classification rates for SC samples indicate that the population at the southern distributional boundary is probably supplied to some degree with adult individuals from lower latitudes. In fact, *C. faber* appears to display a seasonal movement in the SBB, as suggested by monthly fishery landings (PMAP-BS, 2017a, 2017b), providing support for some degree of population mixing in this region. However, the possibility that misclassification among sampled coastal areas may be related to partially homogeneous and similar environmental conditions, as observed for coastal islands from southern Brazil (Daros et al., 2016), cannot be excluded.

In conclusion, the results of this study showed moderate to high phenotypic regional differences between *C. faber* individuals indicating the presence of discrete local populations, and suggest that these fishery areas should be managed in the Southwest Atlantic as different stocks. However, additional data are required to support the observed phenotypic variation in otoliths of *C. faber* across spatial and temporal scales. Since the techniques employed hereby provided a phenotypic marker representative of the fish's entire life-history prior to capture, there are not enough data to unravel when or where such phenotypic distinction among regions was developed (Moreira et al., 2018). Further studies employing similar techniques, but with finer temporal resolution (e.g. ICP-MS-LA), may be useful to track migration routes during *C. faber*'s lifetime and to examine the significance of spawning components in the SSB. In addition, other phenotypic techniques (e.g. morphological analyses and otolith stable isotope analysis) and genetic markers (e.g. microsatellites and SNPs) should be considered to complement this information, especially since the use of a holistic approach maximizes the likelihood of correctly delineating stocks of *C. faber*.

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CAPÍTULO 4

Use of otolith elemental signatures to unravel the life history of the Atlantic spadefish, *Chaetodipterus faber*, in the Southwest Atlantic Ocean

Use of otolith elemental signatures to unravel the life history of the Atlantic spadefish, *Chaetodipterus faber*, in the Southwest Atlantic Ocean

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ABSTRACT

In the current study, otolith fingerprinting was used to test the hypothesis that estuarine systems are effective juvenile habitats for *Chaetodipterus faber* in the Southwest Atlantic Ocean and that this species displays seasonal migrations between estuarine and marine environments. Adults' *C. faber* were collected in euhaline environments from five regions of Brazil and otolith elemental ratios (Sr/Ca, Ba/Ca and Mn/Ca) were recorded from core to otolith edge. Otolith Sr/Ca ratios variation within *C. faber* individuals demonstrated that most fish spend the first year of life within estuaries moving thereafter toward seawater. Two distinct movement patterns were found for *C. faber* throughout lifetime; marine migrants: fish that use estuaries during their juvenile stage and then move towards marine environments; and estuarine visitants: fish that use estuaries during their juvenile stage with fluctuating behavior between estuarine and marine environments during their adult life stage. Marine residence evidence throughout all lifetime was not found. Spawning appears to occur mainly in estuarine and adjacent coastal waters. Moreover, seasonal movements recorded evidenced that inshore (artisanal) and offshore (industrial) fisheries likely require a shared quota. Additional research is however required to evaluate the connectivity between environments, an important pre-requisite to a rational fisheries management of *C.faber*.

Keywords: Ephippidae; SW Atlantic, otolith microchemistry; laser ablation; LA-ICP-MS; salinity migratory behavior.

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1. Introduction

To unravel reef-associated fish movements is an important issue in seascape ecology. However, it has proved difficult, because reef-associated fishes commonly reside in high-diversity systems and complex seascapes where population dynamics are inherently linked to connectivity occurring over many spatial (e.g., habitat, and ecosystem) and temporal (e.g., ecological, and evolutionary) scales (Correia et al., 2012; Mumby and Hastings, 2008; Rooker et al., 2018). The ontogenetic habitat changes include requirements for different food sources, vulnerability to predators, and a need to reproduce in habitats which offer the greatest offspring success (Laegdsgaard and Johnson, 2001; Mumby and Hastings, 2008; Thorrold et al., 2001). In addition, fish movements related to environment gradients (i.e., migration) allow individuals to avoid unfavorable ecological and environmental conditions and can represent the only opportunity to fish reproduction, especially to those who form spawning aggregations (McKeown et al., 2015; Mumby and Hastings, 2008; Rooker et al., 2018).

A broad spectrum of reef-associated fishes, including those of commercial importance (e.g., Lutjanidae, Epinephelidae, and Sparidae) use estuarine littoral habitats during their juvenile stage and then migrate seaward to reef habitat as young adults (Aschenbrenner et al., 2016; Correia et al., 2011; Tzadik et al., 2017). It has been shown, however, that not all fishes dependent on particular nursery but are able to utilize a wide variety of estuarine and marine environments as juveniles (Whitfield and Pattrick, 2015). Effective juvenile habitat (EJH) for a particular species contributes in a greater proportion of individuals to the replenishment of adult population than the mean level contributed by all habitats used by juveniles (Dahlgren et al., 2006), otherwise it may just function as an additional juvenile habitat (Kimirei et al., 2011). To understand the effectiveness of these nearshore habitats as nurseries is important to conservation and restoration issues, namely of critical habitats. A nursery area generally supports higher juveniles densities, allow juvenile fish to avoids predators more successfully, and fish grows more rapidly there than in other habitats (Beck et al., 2001). Additionally, these habitats must have good connectivity corridors to permit successfully habitat shift as fish grow (Gillanders et al., 2003). The level of such connectivity determines, for example, the extent to which demographic processes contribute to populations regulation and replenishment of other fished populations, sometimes distant from juvenile nursery areas (Fowler et al., 2017; Hamer et al., 2011; Mensink and Shima, 2016). A variety of methods has been used to determine movement from juvenile to adult habitats including distribution, abundance and size structure, spatial partitioning of maturity, internal and external tags, stable isotopes and otolith elemental signatures (Gillanders et al., 2003). Among these methods,

otolith elemental signatures offer a direct measure of EJH (Dahlgren et al., 2006) providing a high resolution of temporal and spatial fish movements (Correia et al., 2014).

Otoliths are considered to be metabolically inert structures that grow continuously throughout the fish's life accreting trace elements from the environment where fish lived (Campana et al., 2000; Campana and Neilson, 1985; Hamer et al., 2006). In the past years, otolith elemental fingerprints have helped researchers to unravel migratory and non-migratory behavior (or partial migration) of fishes by tracing elemental concentrations along chronological marks (e.g., growth increments) within the otoliths (Daros et al., 2016; Fowler et al., 2016; Tzadik et al., 2017). Some elements, such as strontium (Sr) and barium (Br), display high correlations between environmental and otolith concentration (Albuquerque et al., 2010; Bath et al., 2000; Webb et al., 2012), being these the most widely applied elements in otolith chemistry (Izzo et al., 2018). Manganese (Mn) has also been included in studies as an environmental indicator, particularly of estuaries (Aschenbrenner et al., 2016; Hanson et al., 2004; Laugier et al., 2015). While Mn water concentrations tend to decrease with distance from coastlines, Sr shows an inverse pattern (Aschenbrenner et al., 2016; Hanson et al., 2004; Laugier et al., 2015; Thomas and Bendell-Young, 1999). However, in addition to physical-chemical properties of the surrounding aquatic environment, the incorporation of different elements in the aragonite matrix of otolith is influenced by multiple factors (e.g., genetic, physiological, and trophic nets) and the effect of salinity on otolith chemistry requires careful consideration (Elsdon et al., 2008; Izzo et al., 2018; Sturrock et al., 2015).

The Atlantic spadefish *Chaetodipterus faber* (Broussonet 1782) is a reef-associated fish, distributed along the tropical and subtropical western Atlantic Ocean, encompassing the Caribbean Sea and Gulf Mexico (Machado et al., 2017; Soeth et al., 2014; Burgess, 2002). The species is fished commercially and recreationally throughout its geographic occurrence range (Bell 2005; PMAP-BS 2017a, 2017b). With a poorly understood migratory behavior (Machado et al., 2017; Soeth et al., 2019b), this euryhaline species has been classified as marine migrants (Barletta et al., 2003), oceanodromous (Reide, 2004), marine stragglers (Araújo et al., 2016; dos Passos et al., 2013), and estuarine transient (Pichler et al., 2015; Possatto et al., 2016). Adults' *C. faber* are benthopelagic and frequently observed in reef environments until to 30-40 meters depth (Hayse 1990; Burgess 2002; Simon et al. 2013; Daros et al. 2012). The presence of large-size *C. faber* within or nearby estuaries appears to be related to their reproduction (Soeth et al., 2019a). In fact, early life stages of *C. faber*, have been collected manly inside or at the entrance to bays and estuarine systems (Barletta-Bergan et al., 2002; Bonecker et al., 2009; Burghart et al., 2014; De Castro et al., 2005; Joyeux et al.,

2004), and in coastal waters and riverine frontal areas (Ditty et al., 1994). Demersal early juveniles are plant mimetics avoiding predation (Barros et al., 2015, 2012) more successfully at regions with large amount plant debris, like estuaries, where *C. faber* juveniles are notably abundant (Barros et al., 2013; Hayse, 1990; Possatto et al., 2016; Soeth et al., 2019a).

Despite some evidence of estuarine use by juveniles, the overall contributions of estuarine areas to the *C. faber* adult populations' replenishment remain unknown. Our understanding of populations dynamics relies on largely untested models of migratory *C. faber* behavior based on the fishing and abundance data, which do not necessarily equate to ontogenetic movements of individuals (Baker et al., 2019; Gillanders et al., 2003). A clear understanding of species movement patterns is critical to a right delineation of marine protect areas which maximize populations resilience in the face of contemporary environmental changes. Therefore, otolith elemental fingerprints were used as natural tags to test the hypothesis that: (1) estuarine systems are effective juvenile habitats for the *C. faber* across Southwest Atlantic Ocean, (2) this species display seasonal migrations and (3) local populations and individual's exhibits no independent migratory dynamics.

2. Material and Methods

2.1 Study area and biological sampling

Fish sampling was conducted in euhaline coastal environments of Southest and South Brazil, including Espírito Santo (ES), Rio de Janeiro (RJ), São Paulo (SP), Paraná (PR), and Santa Catarina (SC) states (Fig. 1). In these regions, the Brazil Current (BC) transports the warm and salty Tropical Water (TW; temperature > 20ºC; salinity > 36) southwestward within the mixed layer (0-200 m) on the continental slope (Castro et al., 2006; Silveira et al., 1994). At thermocline depths, BC transports the South Atlantic Central Water (SACW; temperature between 6ºC and 20ºC >; salinity between 34.5 and 36) (Castro et al., 2006; Piola et al., 2000; Silveira et al., 1994). The cool and less saline Coastal Water (CW), occupying the inner and medium shelf, is formed primarily from river runoff water, estuarine plumes, SACW, and TW (Castro et al., 2006; Castro and Miranda, 1998). Wind-driven coastal upwelling of SACW in large portions of the shelf, especially during the austral summer along narrow continental shelf regions between 20ºS - 23ºS and 28ºS - 29ºS (Fig. 1) (Castro et al., 2006; Emílsson, 1961; Palóczy et al., 2016; Rodrigues and Lorenzzetti, 2001).

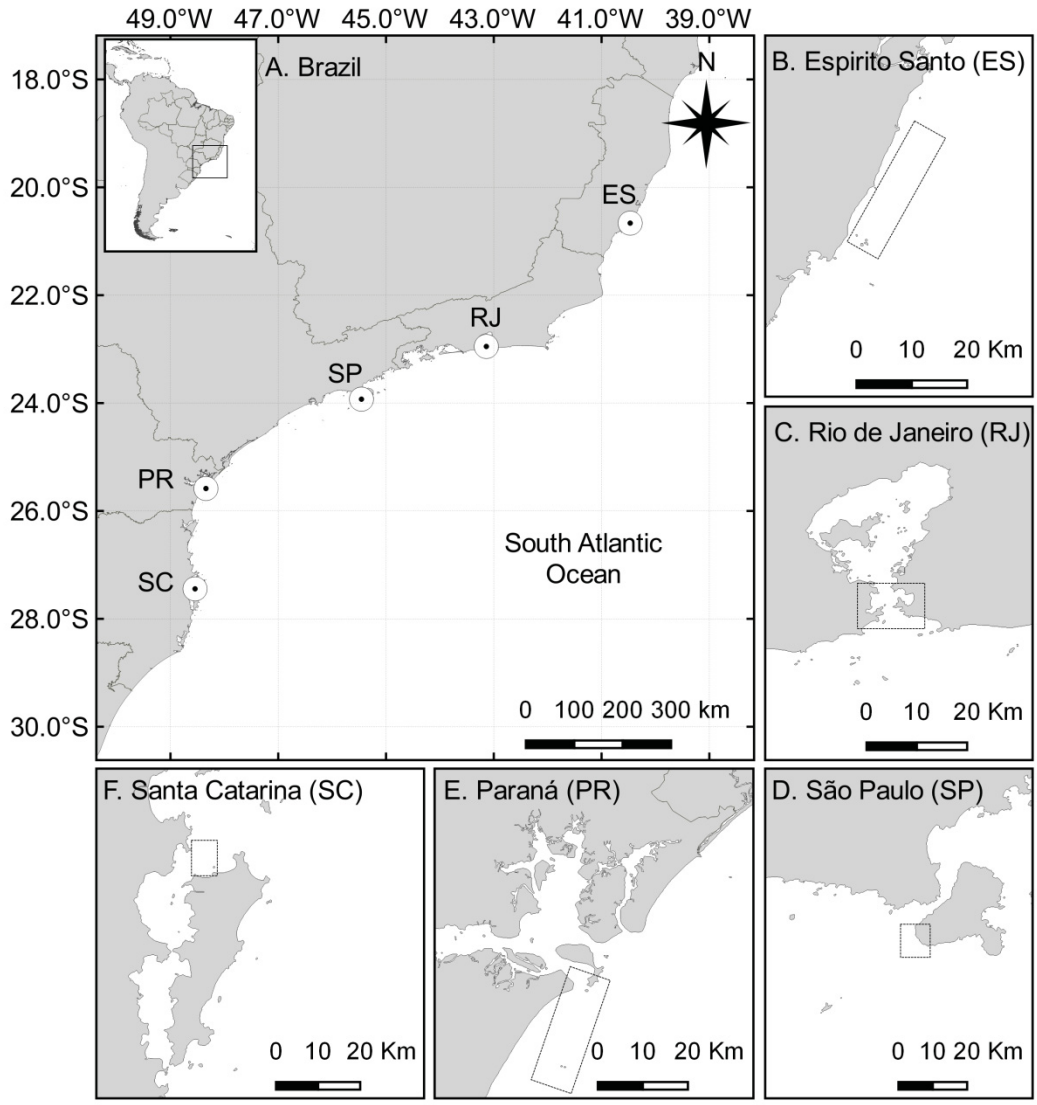

Figure 1. Map of South America (top left) and the Brazilian coast (A) showing (circles) where samples were collected. Rectangles (dashed lines) indicate *Chaetodipterus faber* sampling collection sites; Espírito Santo (B), Rio de Janeiro (C), São Paulo (D), Paraná (E), and Santa Catarina (F).

2.2. Fish sampling and age determination

A total of 75 individuals (15 per site) were collected between December 2015 and March 2016 by spearfishing or obtained from artisanal fishermen using gill nets. Upon collection or immediately after landing, fish were preserved on ice and processed in the laboratory. The individuals were measured for total length (TL, 1 mm) and the gonads were evaluated macroscopically for sex determination and development stages (Soeth et al., 2019a). Sagittal otoliths were removed using plastic forceps then were cleaned of adherent

tissues with ultrapure water (Milli-Q water), dried with lint-free paper, and stored dry in labeled Eppendorf tubes.

Left otoliths were embedded in transparent epoxy resin (Buhler, Epothin), and were cut near the nucleus (0.5 mm) with a diamond saw (Buhler, Isomet Low-Speed Saw). Otolith cross-sections were ground along the transverse plane to expose the core with 400, 1200 and 2400 silicon carbide papers (Buehler, Epothin) and further polished with 6, 3, 1 μm diamond pastes on lapping cloth (Metadi II, Buehler) (Correia et al., 2014). Age estimation of transverse otolith cross-sections was made using an established protocol for *C. faber* (Davies et al. 2015). The annual growth pattern increment deposition was recently validated by Soeth et al. (2019a).

2.3 Microchemical analysis

Otolith microchemistry (^{43}Ca, ^{55}Mn, ^{88}Sr, and ^{138}Ba) was used in order to examine movement behaviors of the *C. faber*. The otoliths cross-sections were attached on a glass slide with epoxy resin (Buhler, Epothin) and cleaned in an ultrasonic bath with ultrapure water (Milli-Q water) for five minutes, then rinsed with Milli-Q water, and dried in a laminar flow hood (Correia et al., 2014). Isotopic elemental concentrations in otolith cross-sections were measured using a 193nm ArF* Excimer Laser Ablation System (LA, Photon Machines Analyte G2) coupled to an ICP-MS Agilent 7700 (Agilent Technologies) at University of Oviedo, Spain. The abundances of isotopes ^{43}Ca, ^{55}Mn, ^{88}Sr and ^{138}Ba were determined from the core to the edge of otolith sections along the ventral axis in one continuous transect (Fig. 2). LA settings were: beam diameter 50 μm, fluence 12 J cm^{-2}, repetition rate 10 Hz, scan speed 10 μm s^{-1}, and energy output 100% (5.6 mJ maximum). Helium was used as the carrier gas in the ablation which was mixed with argon for injection to the ICP-MS plasma, which operated at nebulizer gas flow of 0.9 L min^{-1}. ^{43}Ca was used as the internal standard with a concentration in the otolith matrix estimated in 36%. SRM NIST 612 silicate glass (National Institute of Standards and Technology; www.nist.gov) was analyzed throughout each six otoliths in order to (1) calibrate the conversion between counts per second to elemental concentration relative to a standard chemical element (mol/mol), and (2) to correct for machine drift and mass bias (Sirot et al., 2017; Webb et al., 2012). In order to avoid any surface contamination, a pre-ablation of 85 μm was run prior to the main 50 μm transects. Before each ablation, 30 seconds of background chemical signals were measured for each isotope with the laser switched off. The background average value was used as a blank

correction of subtracting from the signal recorded during laser ablation (Sirot et al., 2017). The average relative standard deviation for 20 NIST 612 transects of two millimeters each was less than 5% regardless the element with a value of recovery obtained ranging between 82% and 100%. All isotope data are given as concentration relative to ^{43}Ca (element/Calcium). For presentation, ratios were converted to mmol mol^{-1} for Sr/Ca and to µmol mol^{-1} for Ba/Ca and Mn/Ca. Codes of samples start with the region of collection.

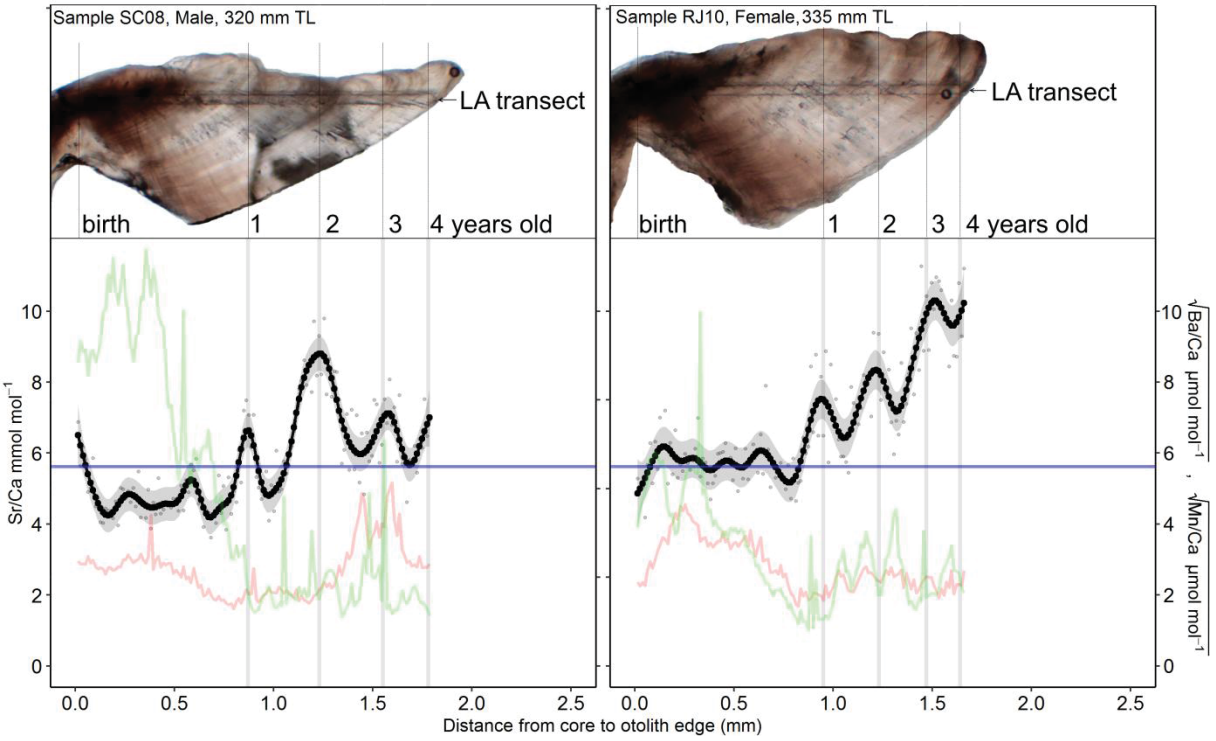

Figure 2. Representative laser ablation transects along the growth axis of two *Chaetodipterus faber* with chronological marks (annuli formation, vertical gray bars) superimposed on data. The grey dots indicate each otolith Sr/Ca ratio point value, while the solid black line with black circles and gray shading indicate the fitted GAM and 95 % Bayesian confidence intervals, respectively. Otolith Mn/Ca (green line) and otolith Ba/Ca (red line) profiles were square root scaled to allow resolution of variation with otolith Sr/Ca data. Horizontal blue line indicates estuarine-marine thresholds for otolith Sr/Ca ratios. Note that each code of samples start with the region of collection.

Ablated otoliths cross-sections were photographed using a microscope with transmitted light coupled to a 5 megapixels Opticam (OPT5000 Power) at 40x magnification. Laser transects were measured using the software ImageJ (IJ 1.46r version) and ablation time was converted to distance from core to edge of otoliths (Fig. 2).

2.4 Data analyses

In order to identify salinity environments and to reconstruct the history of *C. faber* regarding habitat use, the Sr/Ca ratio on the edges (last laser spot) of otoliths was assumed to represent the capture environment (Albuquerque et al., 2012; Avigliano et al., 2017a; Schilling et al., 2018; Tabouret et al., 2010). Mean otolith edges Sr/Ca ratio from samples obtained by spearfishing in marine environments from ES (n = 15, salinity 36.4), SP (n = 15, salinity 35.5) and PR (n = 15, salinity 35.3) were used as reference criteria. Samples obtained from artisanal fishermen (RJ and SC) were not used for this propose. The transition threshold between seawater (i.e., euhaline waters) and estuary or brackish water (i.e., polyhaline waters) was calculated as the mean of the otolith edge Sr/Ca ratios from reference samples minus the standard deviation multiplied by 1.5 [i.e., mean – (1.5 * SD)], similar approach used by Tabouret et al. (2010) and Avigliano et al. (2017a).

To evaluate whether annuli formation occurs at similar distances from core among regions a permutational univariate analysis of variance (PERANOVA) were performed using PRIMER 7 v.7.0.13. Differences in element/Ca ratios averaged by age and among sampling regions were also analyzed by PERANOVA. The mean distance of annuli from core was used as a proxy for the age when cross-sections poor legibility of annuli not allowed to estimate the fish age. PERANOVA dissimilarity matrices were based on Euclidean distance, and p-values were generated using 9999 permutations. The correlation between otolith elements/Ca ratios across sampling regions were assessed by Spearman correlation coefficient (Avigliano et al., 2017a; Fowler et al., 2016).

Sr/Ca ratio variation from the core to otolith edge of *C. faber* were analyzed by Generalized Additive Models (GAMs) implemented with the MGCV package in R programming language (R Development Core Team, 2017). GAMs are nonparametric and useful for describing nonlinear relationships between variables. In addition, GAM attenuates the signal fluctuations during laser ablation allowing better visualization of the profiles and migratory standards. Models were fitted using a Gaussian distribution (identity link) and thin-plate regression spline smoothing functions. The basis dimension (k) for the smooth [i.e., the maximum possible effective degrees of freedom (edf) allowable for a smooth term in the model] was defined by the empirical formula $k = 10N^{2/9}$, where N is the number of data in each profile (Brennan et al., 2015; Kim and Gu, 2004). The edf was controlled by the degree of penalization selected during fitting by generalized cross-validation (GCV). The higher the edf, the more non-linear is the smoothing spline. Therefore, edf value was used as an indication of how variable each Sr/Ca profile was. Confidence intervals (95%, C.I.) to GAM

and p-values were obtained by a Bayesian approach (Marra and Wood, 2012) and were used to determinate where (profile distance) and when (age) significant shifts in the Sr/Ca ratio occurred (Brennan et al., 2015). For graphical presentations Ba/Ca and Mn/Ca ratios were displayed with square root transformation owing to the order of magnitude variation (Hamer et al., 2015).

The environmental histories of *C. faber* across entire otoliths were used to classify the individuals as Marine Resident (MR), Marine Migrant (MM) and Estuarine Visitor (EV). Individuals were classified as MR when otolith Sr/Ca ratios were maintained at marine levels, as MM when otolith Sr/Ca ratios were maintained at brackish levels at the age-0 group (young-of-the-year) and changed to otoliths Sr/Ca ratios seawater levels towards the otolith edges. Individuals in which the otolith Sr/Ca ratios oscillate more than once between the estuarine and marine threshold were classified as EV (Franco et al., 2018).

To estimate the time at which 50% (T_{50}) of individuals egress from estuarine to marine environments (Albuquerque et al., 2012) otolith Sr/Ca ratios was converted to binary environment determinations (0 = estuarine, 1 = marine). A bias-reduction generalized linear model with binomial responses (brglm) and logit-link (Kosmidis, 2014) implemented with the brglm package in R programming language (R Development Core Team, 2017) was used to estimate the time of estuarine egress. The distance from the otolith core was used as a predictor variable (i.e., a proxy of age). Graphics results are shown with the mean age estimated in the upper axis for better ecological interpretation.

3. Results

3.1 Age estimates and annuli measures

Age estimates from otoliths cross-sections and TL ranged from 2 to 7 years and 272 to 475 mm, respectively (Table 1). Otolith cross-sections from SC, PR, and SP were largely readable (100%). To RJ and ES otolith cross-sections poor legibility of annuli was found and only 47% (RJ) and 27% (ES) otoliths were aged successfully (Table 1). The first and subsequently annuli formation showed similar distances from core at LA transects among regions (PERANOVA, pseudo-F = 1.56; df = 4; $p > 0.05$). Therefore, the distances of annuli formation from core (mean ± S.D) for pooled regions were 0.85 ± 0.13 mm (1st annuli), 1.30 ± 0.16 mm (2nd annuli), 1.61 ± 0.17 mm (3rd annuli), 1.81 ± 0.20 mm (4th annuli), 1.95 ± 0.25 mm (5th annuli), 2.07 ± 0.13 (6th annuli), 2.11 ± 0.05 mm (7th annuli) and 2.18 ± 0.03 mm (8th

annuli). Macroscopic evaluation indicated that all individuals sampled were adults (spawning capable phase). However, fish sex was no took into account in the hereby analyses.

Table 1. Sample size (n), total length (TL), age of *Chaetodipterus faber* by sampling region [Mean (±SD, standard deviation) and range (minimum and maximum)]. Espírito Santo (ES); Rio de Janeiro (RJ); São Paulo (SP); Paraná (PR); Santa Catarina (SC).

Region	n	TL (mm)		Age (years)	
		Mean±SD	Range	Mean±SD	Range
ES	15	354 ± 36	320 - 475	5.0 ± 1.6	3 - 7
RJ	15	334 ± 17	310 - 373	3.7 ± 0.5	3 - 7
SP	15	320 ± 24	281 - 360	3.0 ± 0.5	2 - 4
PR	15	397 ± 24	354 - 448	4.3 ± 0.9	3 - 7
SC	15	316 ± 22	272 - 345	3.8 ± 0.7	3 - 5

3.2 Otolith elemental composition

The otolith Sr/Ca ratios ranged from 2.97 mmol mol^{-1} to 15.54 mmol mol^{-1} (mean ± SD: 5.89 ± 1.65 mmol mol^{-1}), while otolith Ba/Ca and Mn/Ca ratios ranged broader, from 3.15 µmol mol^{-1} to 1,420 µmol mol^{-1} (mean ± SD: 11.39 ± 33.30 µmol mol^{-1}) and from 0.35 µmol mol^{-1} to 1,684 µmol mol^{-1} (mean ± SD: 11.39 ± 33.30 µmol mol^{-1}), respectively (Fig. 3). Differences among regions and age were significant (PERANOVA, $p < 0.01$) for all three otolith trace elements analyzed (Table 2). Estimates of components of variation showed that otolith Sr/Ca and Mn/Ca ratios variation were mainly explained by fish age (>45%), while sampling region explained less than 14% of the variation accounted by the PERANOVA model. For otolith Ba/Ca ratios more than 64% (residuals) of the variation was not explained by the model terms, indicating that otolith Ba/Ca ratios, opposite to otolith Sr/Ca and Mn/Ca ratios, could be problematic to interpreted in a more ontogenetic meaningful way. Otolith Sr/Ca ratios were negatively correlated (Spearman correlation, $p < 0.05$) with the otolith Mn/Ca ratios in all sampling regions (Table 3). In contrast, no consistent correspondence was found between otolith Sr/Ca and Ba/Ca ratios as positive (ES, SP, and PR), negative (RJ) e no correlation (SC) were recorded across sampling regions (Table 3).

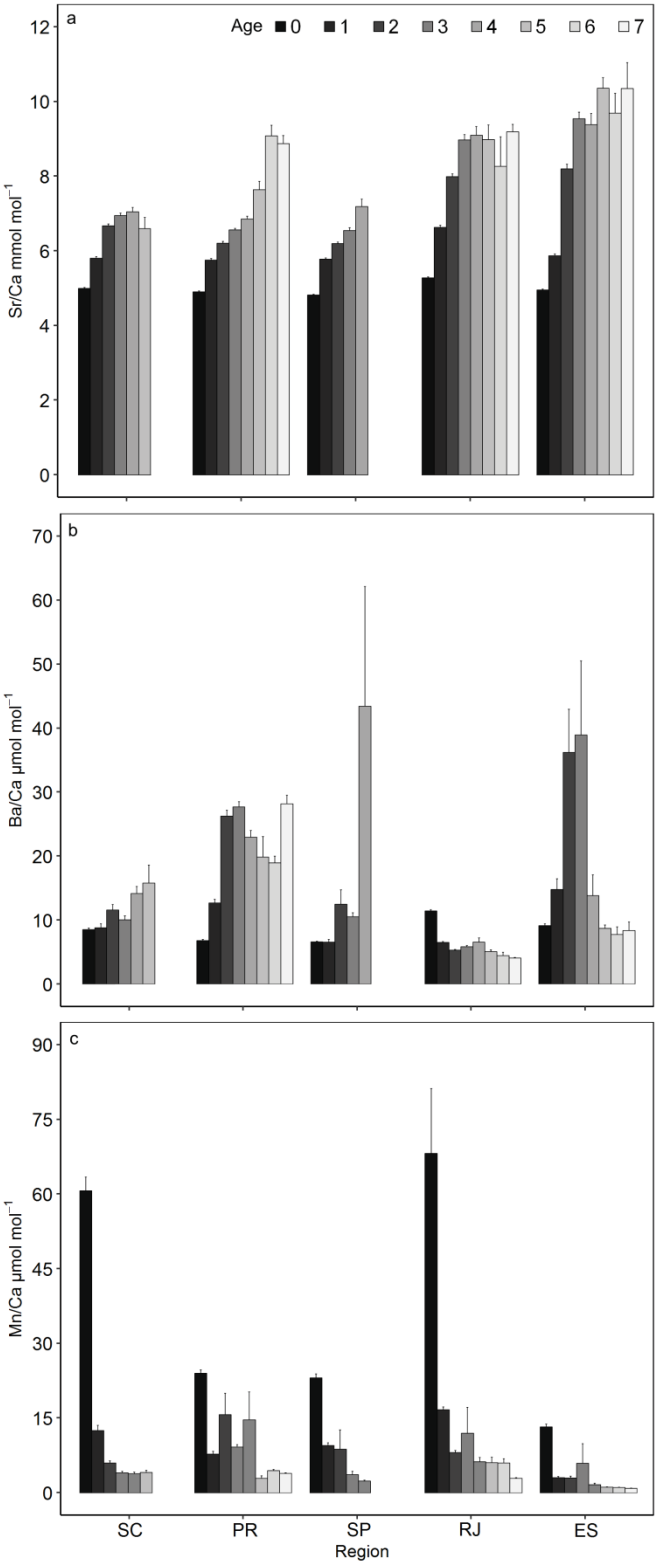

Figure 3. Regional and age comparison (mean ± SE) of otolith Sr/Ca ratios (a), Ba/Ca ratios (b), and Mn/Ca ratios (c) from *Chaetodipterus faber* caught in euhaline coastal areas of Espírito Santo (ES), Rio de Janeiro (RJ), São Paulo (SP), Paraná (PR), and Santa Catarina (SC).

Table 2. Regional and age comparison of element/Ca ratios profiles (averaged by age) by permutational univariate analysis of variance from *Chaetodipterus faber* caught between December 2015 and March 2016 in coastal areas of Espírito Santo, Rio de Janeiro, São Paulo, Paraná, and Santa Catarina, Brazil. * = $p < 0.01$; ** = $p < 0.001$.

Variable	Source	df	MS	Pseudo-F	ECV (%)
Sr/Ca	Region	4	0.28	22.84**	13.63
	Age	7	1.11	91.85**	55.32
	Region x Age	23	0.05	3.92**	6.98
	Residual	331	0.01		24.07
Ba/Ca	Region	4	3.2	9.19**	13.76
	Age	7	1.43	4.11*	5.1
	Region x Age	23	1.23	3.54**	16.34
	Residual	331	0.35		64.81
Mn/Ca	Region	4	6.71	17.37 **	14.51
	Age	7	21.45	55.53**	47.16
	Region x Age	23	0.86	2.22*	4.15
	Residual	331	0.39		34.19

Table 3. Spearman correlation (*r*) between otolith element/Ca ratios of *Chaetodipterus faber* by sampling region. Espírito Santo (ES), Rio de Janeiro (RJ), São Paulo (SP), Paraná (PR), and Santa Catarina (SC). Significant ($p < 0.05$) correlations are indicated by asterisk (*).

Variable	ES	RJ	SP	PR	SC
r (Sr,Ba)	0.411*	-0.429*	0.165*	0.541*	-0.015
r (Sr,Mn)	-0.441*	-0.609*	-0.483*	-0.319*	-0.595*
r (Mn,Ba)	0.039	0.634*	0.163*	0.072*	0.268*

3.3 Otolith elemental profiles

The Sr/Ca ratio (mean ± SD) on the edges of otoliths from fish captured by spearfishing in seawater environments was 8.11 ± 1.65 mmol mol^{-1}. In the current study a positive relationship between *C. faber* otolith Sr/Ca ratios and water salinity was assumed to

be positive and existent. Therefore, any otolith Sr/Ca ratio below 5.62 mmol mol^{-1} was used to identify movement into a brackish or estuarine environment.

For all *C. faber* otoliths, the distance from core was a significant predictor of otolith Sr/Ca ratio variation (GAM $p < 0.001$; Supplementary table 1). Most of individuals had a similar pattern in the otolith Sr/Ca ratios in their early life. Over 70% of the profiles showed otolith Sr/Ca ratio estuarine signature at the beginning of the profiles. A smaller fraction of samples (<30%), showed otolith Sr/Ca ratio at the beginning of the profiles indicating seawater signature, which then declined quickly to estuarine levels until 0.15-0.4 mm from the otolith core. This pattern was more and less evident from RJ and PR samples, being recorded in 47% and 7% of samples, respectively (Fig. 4, Supplementary file 2 and 4). Changes in otolith Sr/Ca ratio near the core when the fish were less than 1 year old were often between the thresholds expected for fish residing in estuarine habitats (Fig. 4; Fig. 5; Fig. 6; Supplementary files 1, 2, 3, 4, and 5) but not always (e.g., Fig. 2 – Sample RJ10; Fig. 4 - Sample PR02). Superimposing chronological marks of otolith and fitted GAMs, the *C. faber* tended to exhibit the greatest changes in Sr/Ca ratios (at 95% Bayesian confidence intervals) in median and outer regions of the otoliths (>0.85 mm or >1 year old) that were often with a regular time interval of one year (Fig. 2). A fast increase of otolith Sr/Ca ratio were generally accompanied by a sharp decrease of otolith Mn/Ca ratios, namely in RJ and SC samples where the highest negative correlation between these elements/Ca ratio were found (Table 3; Fig. 4 and Fig. 6; Supplementary files 2 and 5). A coincident abrupt increase in otolith Sr/Ca and Ba/Ca ratios were common in outer portions of the otoliths from ES; the levels of Sr/Ca ratios increased around two-fold over the mean otolith edge values, while Ba/Ca ratios increased by over 20 orders of magnitude sometimes (Fig. 6 – Sample ES13; Supplementary file 1). In contrast, no expressive change was found to Mn/Ca ratios at these otolith portions in question. Unidirectional otolith Sr/Ca ratio increase throughout life history was found in one individual only (Fig. 6, Sample RJ02) which showed the smallest effective degree of freedom between samples (GAM $p < 0.001$; edf = 7.42; Supplementary table 1).

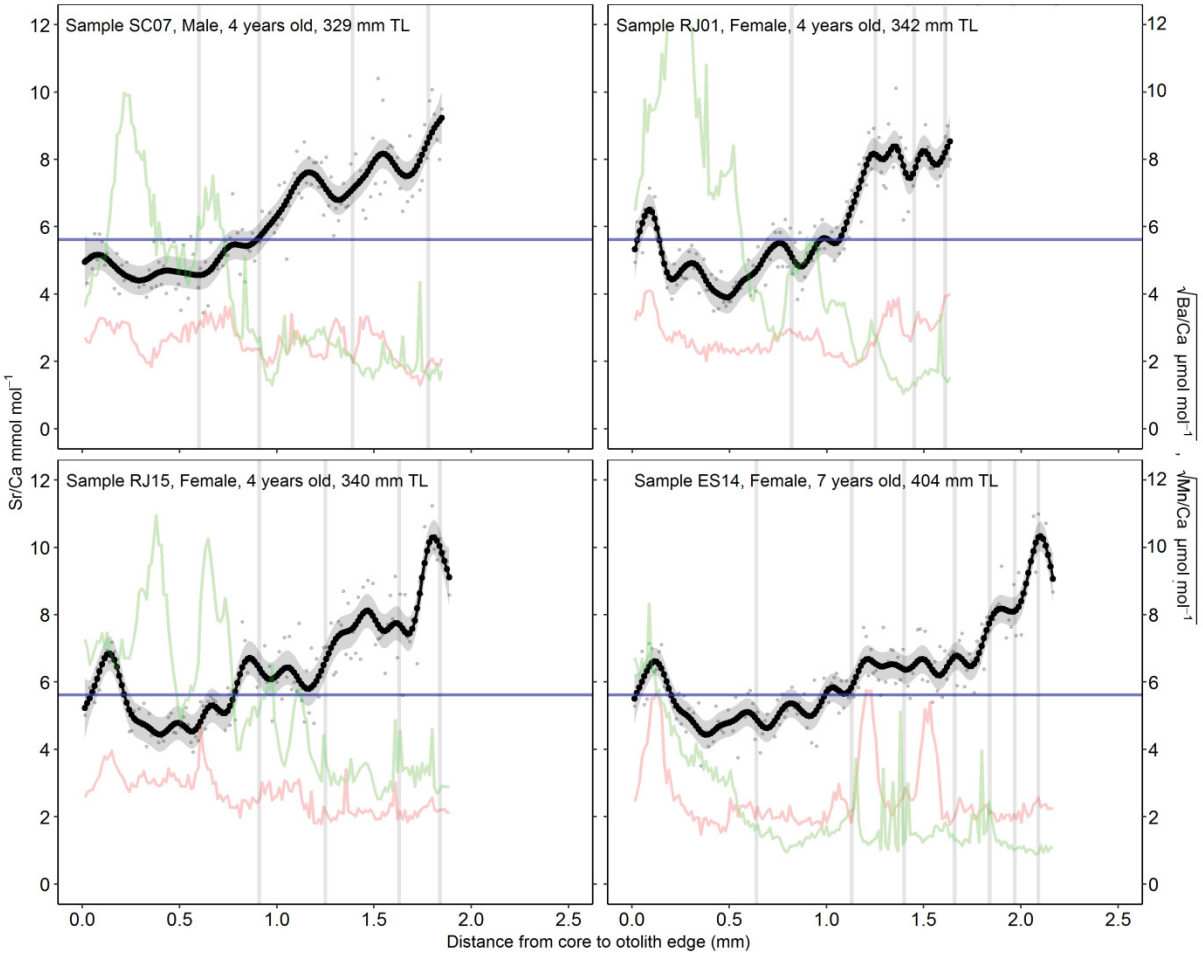

Figure 4. Otolith microchemical profiles of four *Chaetodipterus faber* classified as Marine Migrants. The grey dots indicate each otolith Sr/Ca ratio point value, while the solid black line with black circles and gray shading indicate the fitted GAM and 95 % Bayesian confidence intervals, respectively. Otolith Mn/Ca (green line) and otolith Ba/Ca (red line) profiles were square root scaled to allow resolution of variation with otolith Sr/Ca data. Horizontal blue line indicates estuarine-marine thresholds for otolith Sr/Ca ratios. Vertical gray bars represent the age of the *C. faber* regarding the distance from otolith core. Note that each code of samples start with the region of collection.

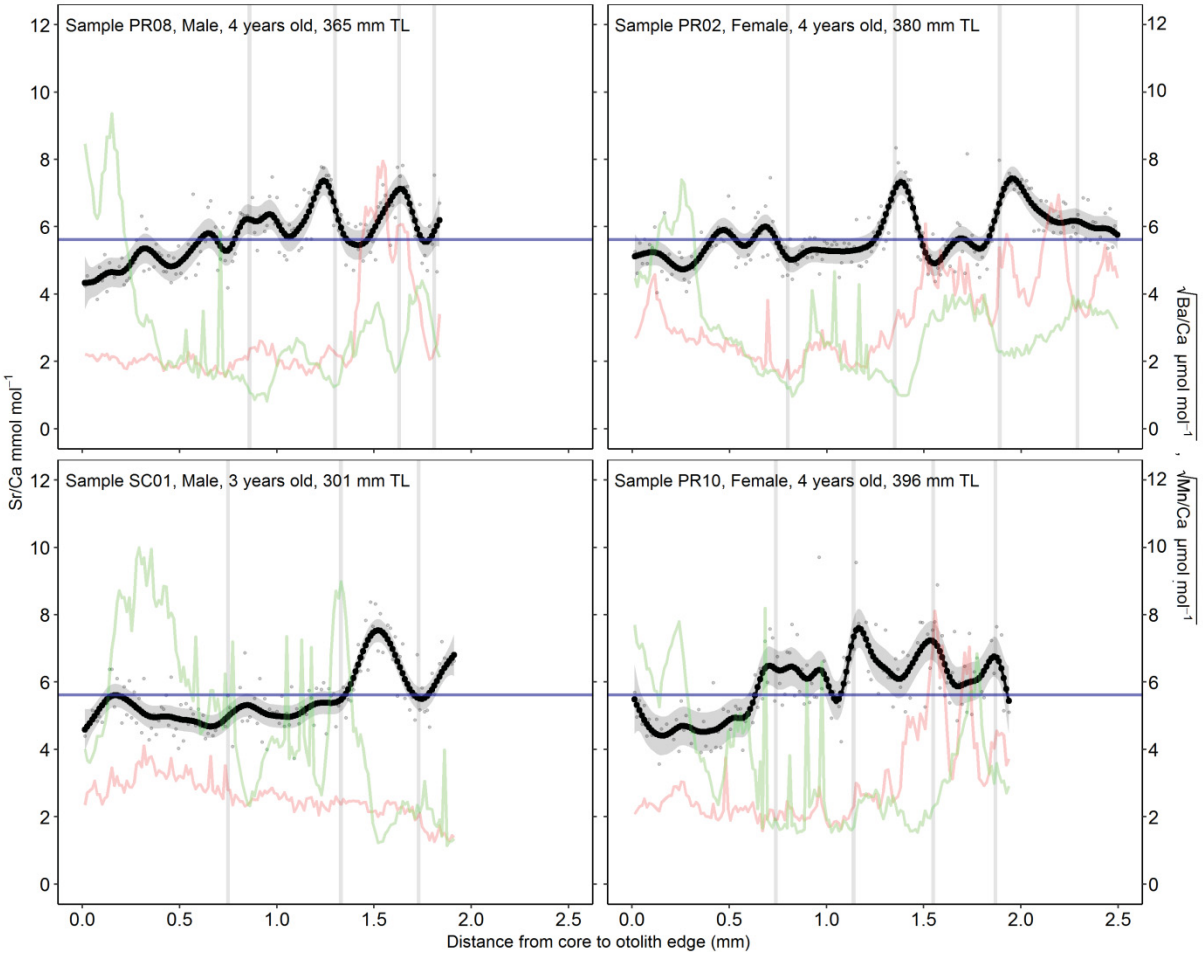

Figure 5. Otolith microchemical profiles of four *Chaetodipterus faber* classified as Estuarine Visitors. Legend for graphical interpretation can be found in figure 2. The grey dots indicate each otolith Sr/Ca ratio point value, while the solid black line with black circles and gray shading indicate the fitted GAM and 95 % Bayesian confidence intervals, respectively. Otolith Mn/Ca (green line) and otolith Ba/Ca (red line) profiles were square root scaled to allow resolution of variation with otolith Sr/Ca data. Horizontal blue line indicates estuarine-marine thresholds for otolith Sr/Ca ratios. Vertical gray bars represent the age of the *C. faber* regarding the distance from otolith core. Note that each code of samples start with the region of collection.

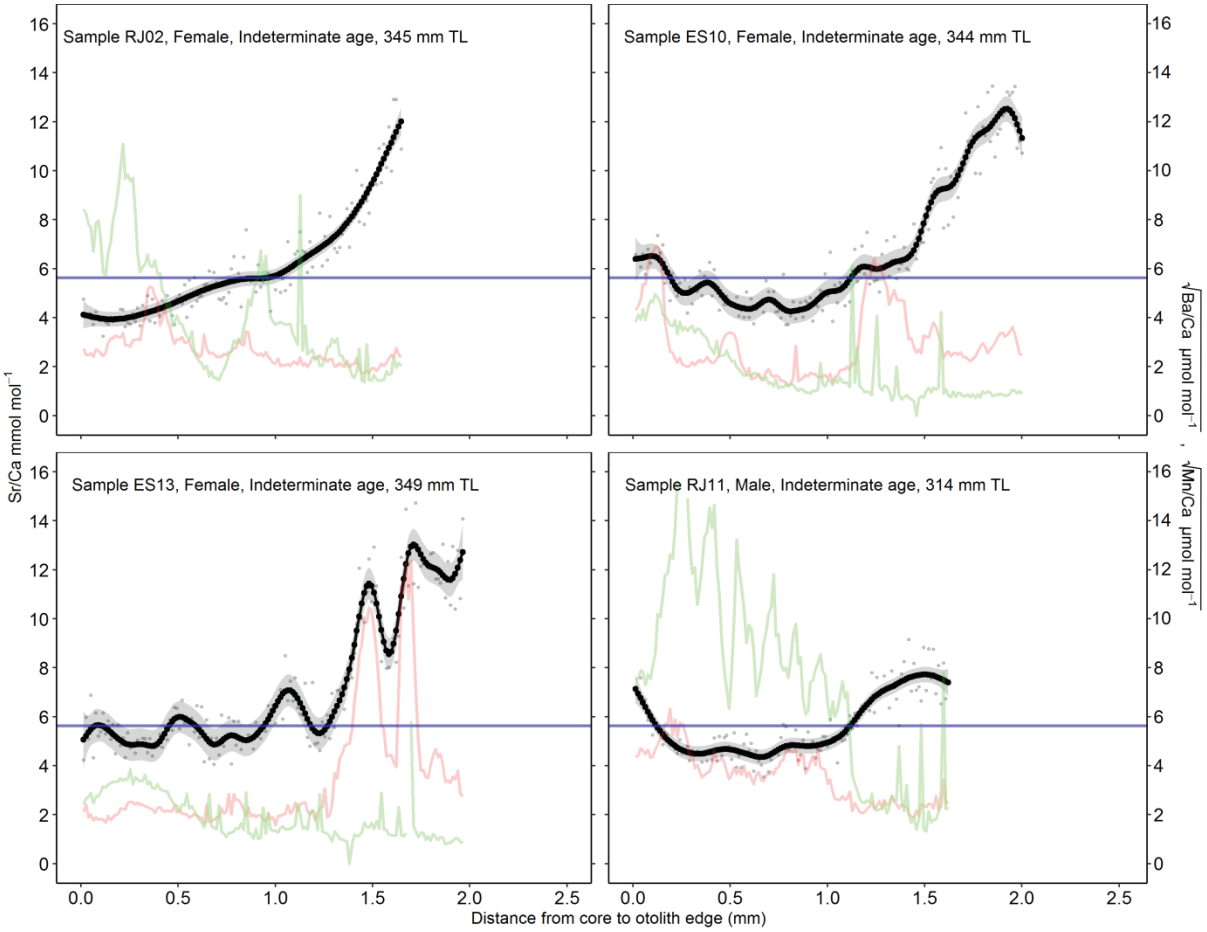

Figure 6. Otolith microchemical profiles of *Chaetodipterus faber* showing unidirectional increasing of Sr/Ca ratio (A), and a positive (B, C) and a negative (d) correlation between otolith Sr/Ca and Ba/Ca ratios. The grey dots indicate each otolith Sr/Ca ratio point value, while the solid black line with black circles and gray shading indicate the fitted GAM and 95 % Bayesian confidence intervals, respectively. Otolith Mn/Ca (green line) and otolith Ba/Ca (red line) profiles were square root scaled to allow resolution of variation with otolith Sr/Ca data. Horizontal blue line indicates estuarine-marine thresholds for otolith Sr/Ca ratios. Vertical gray bars represent the age of the *C. faber* regarding the distance from otolith core. Note that each code of samples start with the region of collection.

The otolith Sr/Ca ratio profiles from *C. faber* sampled in euhaline environments allowed identifying two migratory patterns and different trends among regions (Fig. 7). Marine migrants (MM) were the typical life history of the *C. faber* from RJ (100% of the individuals), ES (86.4%), SC (66.6%) and SP (53%) that showed otolith Sr/Ca ratios ranging

from 3.15-15.54 mmol mol^{-1}, 3.18-13.55 mmol mol^{-1}, 3.20-9.22 mmol mol^{-1}, and 3.33-10.40 mmol mol^{-1}, respectively. The vast majority of samples from RJ and ES showed a sharp increase of otolith Sr/Ca ratios at about 1-1.5 mm from the core (1 to 2 years old) with Sr/Ca ratios increasing around two-fold and remaining at high levels (Fig. 4 and 6). Estuarine visitors (EV) were dominant life history of the *C. faber* from PR region only (53%) where otolith Sr/Ca ratios ranged from 2.97-10.05 mmol mol^{-1}. Otolith Sr/Ca ratios from EV varied significantly (at 95% C.I.) but rarely again descended at otolith age-0 mean levels (~5 mmol mol^{-1}) after reach marine otolith Sr/Ca ratios signatures (Fig. 5) indicating that adults remain in outer estuarine areas while juveniles individuals likely to remain in less saline environments. No individual was classified as Marine Resident (MR).

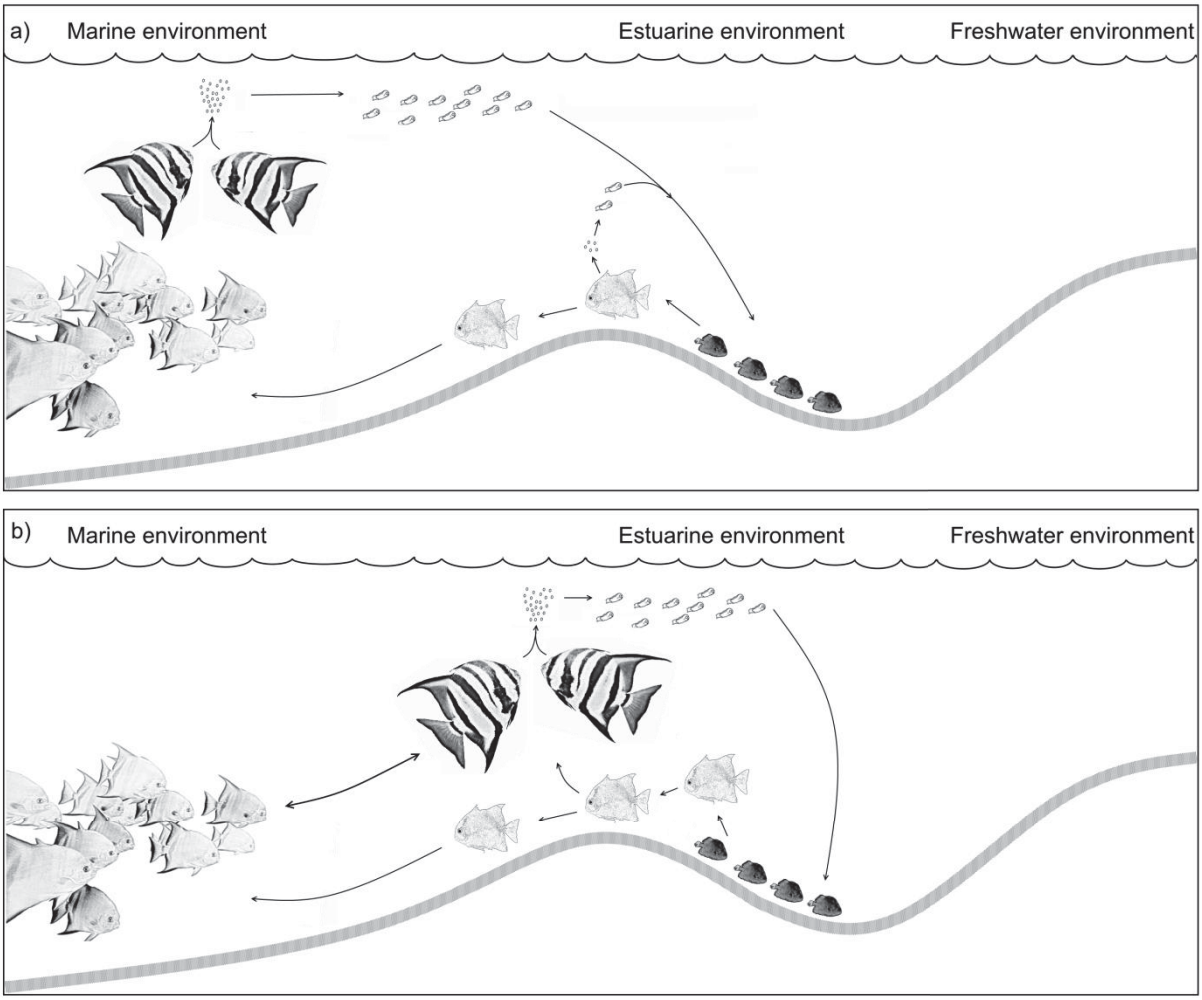

Figure 7. Reconstruction of *Chaetodipterus faber* migration derived from otoliths element/Ca ratios signatures. (a) Marine migrants, and (b) Estuarine visitors. Scheme modified from Elliott et al. (2007).

The bias-reduction generalized linear model with binomial responses estimated a mean estuarine egress (T_{50}) relative to otolith size (i.e., distance from otolith core) of (mean ± standard error) 1.01 ± 0.01 mm for pooled data, representing mean estuary residence from 1 to 2 years (Fig. 8).

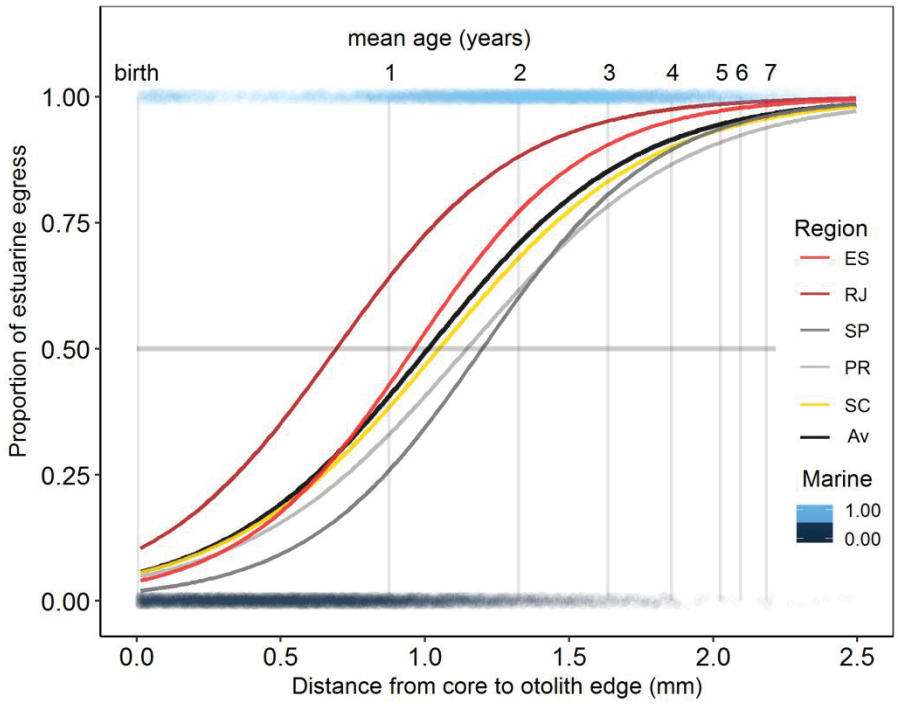

Figure 8. Bias-reduction generalized linear model with binomial responses for the estimated proportion of the mean estuarine egress of *Chaetodipterus faber* relative to otolith size (i.e., distance from otolith core). Horizontal gray bar represents the otolith size when 50% of the individuals (T_{50}) emigrate from estuarine to marine environments, which were (T_{50} ± standard error): 0.96 ± 0.02 mm (ES), 0.69 ± 0.02 mm (RJ), 1.19 ± 0.02 mm (SP), 1.15 ± 0.02 mm (PR), 1.05 ± 0.02 mm (SC), and 1.01 ± 0.01 mm for pooled data (Av), which represents an age between 1 and 2 years old. Vertical gray bars represent the mean age of the *C. faber* regarding the distance from otolith core in coastal areas of Southwest Atlantic Ocean.

4. Discussion

This study intended to track migration through different salinity environments during the *Chaetodipterus faber*'s lifetime employing microchemical analyses via LA-ICP-MS techniques. Despite there is no experimental validation of the relationship between salinity and otolith element/Ca ratios for *C. faber* or even Ephippidae fishes, mean Sr/Ca ratio in the

seawater zone of otoliths (i.e., otoliths edges) were comparable to values already reported to other teleost's fish otolith residing in marine environments in Southwestern Atlantic Ocean (e.g., about 6 to 10 mmol mol^{-1}), including *Epinephelus marginatus* (Epinephelidae, Condini et al., 2016), *Stegastes fuscus* and *Abudefduf saxatilis* (Pomacentridae, Adelir-Alves et al., 2019; Daros et al., 2016), *Genidens baurbus* (Ariidae, Avigliano et al., 2017a), *Mugil liza* (Mugilidae, Callicó Fortunato et al., 2017a), and *Micropogonias furnieri* (Sciaenidae Albuquerque et al., 2012; Franco et al., 2018). Interpreting the data under the hypotheses of positive relationship between otolith Sr/Ca ratio and water salinity (as a proxy for water Sr/Ca ratio), the otolith Sr/Ca ratio variation within individuals examined should represent individuals inhabited brackish (i.e., estuary) and marine environments throughout the life history (Avigliano et al., 2017a; Chang and Iizuka, 2012; Fowler et al., 2016; Franco et al., 2018). In the present study, the otolith Sr/Ca ratio threshold between estuarine and marine habitats (5.62 mmol mol^{-1}) was empirically established following previously published similar approaches used to delimitate salinities environments (Avigliano et al., 2017a; Tabouret et al., 2010). This threshold value was similar to other euryhaline species, such as, 6.4 mmol mol^{-1} for *Mugil cephalus* (Fowler et al., 2016), 5.98 mmol mol^{-1} for *Genidens barbus* (Avigliano et al., 2017a), and 6 mmol mol^{-1} for *Micropogonias furnieri* (Franco et al., 2018).

Based on the marine otolith Sr/Ca ratios signature obtained hereby, no individual *C. faber* was classified as Marine Resident. In the past decades the Fish Ecology Laboratory (FEL) from the Center of Studies of the Sea (CEM/UFPR) have investigated the fish assemblages over a complete salinity gradient (0–36) in the main coastal estuarine systems from PR and SC regions (e.g., Paranaguá Estuarine Complex, Babitonga Bay, North and South Bays of Florianópolis), for example, see Cartagena et al. (2011), Pichler et al. (2015), Possatto et al. (2016), Soeth et al. (2014), and Vilar et al. (2011). Spatial analyses of size structure and abundance of the FEL data in relation to water salinity indicate ontogenetic movements of *C. faber*, as individuals caught in estuarine zone were mostly demersal mimetic juveniles (mean ± SD, 56 ± 27 mm TL) and its occurrence was limited to salinities ranging from 15 to 36 (mean ± SD, 27 ± 5.2). This salinity range agrees well with experiments for aquaculture purposes that showed that *C. faber* juveniles can grow and survive in salinities from 15 to 35 (Senett et al., 2011). However, bottom trawl and small seine nets were the main sampling gears used in FEL studies and are likely ineffective to catch benthopelagic adults *C. faber*, indicating that observed size structure does not necessarily equate to ontogenetic movements of individuals (Baker et al., 2019; Gillanders et al., 2003). Despite that, the spatial

size structure agrees well with elemental/Ca profiles recorded in the present study where consistent lower otolith Sr/Ca ratios in otolith's portions representing the early life stages. In addition, the otolith Mn/Ca ratios showed an inverse pattern to otolith Sr/Ca ratios and support an evidence of estuarine use encompassing the first stages of life (Aschenbrenner et al., 2016; Hanson et al., 2004; Laugier et al., 2015). Otolith Mn/Ca ratios has been positively correlated with water Mn/Ca ratios (Dorval et al., 2007; Sturrock et al., 2015) being particularly high in fish otolith inhabiting estuarine environments (Aschenbrenner et al., 2016; Hanson et al., 2004; Laugier et al., 2015). Mn is rapidly precipitated in the marine environment (Thomas and Bendell-Young, 1999) but trophic transfer and habitat constituents may be considered potential Mn sources to fish otoliths (Sanchez-Jerez et al., 2002). Moreover, maternal effects increase the levels of near-primordiun Mn/Ca ratios (Brophy et al., 2004), but outside of this otolith zone (<0.01 mm) its reflects ambient Mn concentrations and trophic nets (Bouchard et al., 2015; Sanchez-Jerez et al., 2002; Sturrock et al., 2015). Disentangling the relative effect of these factors is impossible at this point but both Mn sources are expected to be incremented in regions of estuarine influence (Aschenbrenner et al., 2016; Sanchez-Jerez et al., 2002; Thomas and Bendell-Young, 1999).

In the present study otolith Ba/Ca ratios demonstrated heterogenic patterns regarding to otolith Sr/Ca ratios correlation and most of otolith Ba/Ca ratios variation was not explained by the age and region factors. Water Ba levels are associated with different sources (Elsdon et al., 2008) that can potentially make it difficult to interpret alone. For instance, estuarine Ba water concentration can increase with the terrestrial runoff (Hamer et al., 2006; Shaw et al., 1998) and typically, under this influence, the ratios of water Ba/Ca and Sr/Ca ratios vary in opposite directions in relation to salinity, more notably, however, at estuarine regions with salinities lower than 20 (Albuquerque et al., 2012; Hamer et al., 2006; Tabouret et al., 2010). In costal and ocean open system dissolved Ba and Sr variability may be attributed to upwelling of cold deep waters (Elsdon et al., 2008; Lea et al., 1989; Woodson et al., 2013). High otolith Sr/Ca and Ba/Ca ratios in oceanodromus and non-dispersing reef fish have been associated with upwelling phenomena, for example to *Acanthochromis polyacanthus* (Kingsford et al., 2009) and *Pomacentrus coelestis* from the central and southern Great Barrier Reef, *Thunnus maccoyii* from the Indian Ocean (Wang et al., 2009), and *Thunnus alalunga* from the South Pacific (Macdonald et al., 2013). In fact, a positive relationship between otolith Sr/Ca and Ba/Ca ratios was predominant among the samples and simultaneous increases of these element/Ca ratios were recorded in outer otolith portions. Following above arguments, this may indicate that *C. faber* individuals had migrated to

upwelling or deep areas of the inner- and middle-shelf between 20°S and 28°S of SW Atlantic Ocean (Acha et al., 2004; Palóczy et al., 2016). The bottom South Atlantic Central Water (SACW) intrusions in the inner- and middle-shelf during summer and spring is an event well documented in the study area (Cerda and Castro, 2014; Palóczy et al., 2016). During these seasons sea surface temperatures can be greater than 27°C but near-bottom (15–30 m) temperatures are often lower than 20°C (Castro, 2014; Cerda and Castro, 2014). Moreover, the benthopelagic and feeding behavior of this species (Hayse, 1990; Burgess, 2002; Simon et al., 2013) and its capture by trawl fisheries (mean TL around 250 mm, M. M. Rotundo, personal communication) within these latitudes and depths (Rotundo et al., 2019) support a hypothesis of SACW intrusions through vertical (deep) or horizontal (upwelling) excursions. As temperature may drive complex endogenous and exogenous interactions on Sr and Ba uptake into otoliths (Izzo et al., 2018; Walther et al., 2010) application of high-resolution $\delta^{18}O$ otolith measurements as a proxy for temperature (Sturrock et al., 2015) may promote a better understanding of *C. faber* residence within the SACW in additional studies.

Similar high otolith Sr/Ca and Ba/Ca ratios have previously been documented for the ES local population using solution based techniques (Soeth et al., 2019b). Moreover, otolith Mn/Ca ratios showed no expressive change at these otolith portions in question. A pattern of brief simultaneous increases in otolith Sr/Ca and Ba/Ca ratios may also results of intrusions in freshwater with low Ca levels and high Sr levels (Hamer et al., 2015) and also may be explained by intrusions in semi-closed hypersaline environments (Gillanders and Munro, 2012; Sales et al., 2016). However, samples from ES and SP were caught in saline waters (35-37), and only a rapid migration from freshwater or hypersaline waters to marine environment with delayed uptake of elemental into the otolith could be an reasonable explanation for this observed pattern at otolith edges from these regions (Elsdon and Gillanders, 2005; Fowler et al., 2016).

Different trends among regions and individual *C. faber* were found. From that classified as EV, a seasonal movement was often identified. Although seascape movements can be difficult to distinguish from changing conditions around a resident fish (Baker et al., 2019; Walther and Limburg, 2012), both monthly fishery landings (PMAP-BS, 2017a,b) and reproductive biology (Soeth et al., 2019a) suggest that *C. faber* display seasonal migrations. The otolith Sr/Ca ratio variation observed often within a year period supports the interpretation that the fish moved between inshore (less saline) and offshore (high saline) waters, a displacement that may be associated to spawning aggregation purposes (Soeth et al., 2019a). The low levels of otolith Sr/Ca ratios at the beginning of the most profiles suggested

that fish were spawned in brackish waters. Early life stages of *C. faber* (eggs, larvae, and newly settled), have been collected manly inside or at the entrance to bays and estuarine systems (Barletta-Bergan et al., 2002; Bonecker et al., 2009; Burghart et al., 2014; De Castro et al., 2005; Joyeux et al., 2004), reinforcing the hypothesis that the presence of large-size *C. faber* within or nearby estuaries is related to their reproduction (Soeth et al., 2019a). A smaller fraction of samples showed otolith Sr/Ca ratio at the beginning of the profiles indicating seawater signature, but declining quickly to estuarine levels, suggesting a coastal spawning and a quick larval/juvenile ingress into estuaries, a common pattern in life cycles of estuarine associated species (Secor and Rooker, 2005).

Although an extensive literature documenting the positive relationship between otolith Sr/Ca ratios and water Sr/Ca ratio exist (Yang et al., 2011), some otolith Sr/Ca ratio variation could have been influenced by physiological processes (e.g., growth and gonad development) and other exogenous factors (e.g., temperature and trophic nets) implying that other factors may act upon the relationships of water Sr concentration and otolith Sr concentration (Izzo et al., 2018; Sturrock et al., 2015; Webb et al., 2012). For example, differentiated Sr incorporation rates may occur between juveniles and adults and between winter and summer as less strontium is likely to be incorporated into aragonitic otoliths during periods with higher otolith accretion rates (e.g., pre maturation life stages and warmer periods) (Catalán et al., 2018; De Pontual et al., 2003; Sadovy and Severin, 1994; Stanley et al., 2015). This assumption may partially explain the close correspondence between the formation of opaque zones, manly deposited in the spring (Soeth et al., 2019a), and observed patterns of Sr/Ca ratio drop in some individuals *C. faber*. In addition, the otolith Sr/Ca ratio variation could also be caused by differences in Sr availability relative to Ca availability in the adult's body (i.e., blood plasma) caused by the remotion of Ca into gametes (Clarke and Friedland, 2004; Sturrock et al., 2015). In Brazil's subtropical latitude, the *C. faber* reaches the sexual maturity between 100 and 150 mm TL (1 to 2 years old) and reproduction occur mainly across the spring and summer (Soeth et al., 2019a) which can physiological-driven otolith Sr/Ca ratio rising (Kalish, 1991). Therefore, while higher otolith accretion rates are likely to drive otolith Sr/Ca ratios drop, the gonad development could potentially increase otolith Sr/Ca ratio within the same period (Elsdon et al., 2008; Kalish, 1991; Sturrock et al., 2015).

The otolith microchemical approach used in this study evidenced that estuarine environments are effective juvenile habitats for the *C. faber* in a widely latitudinal range. The consistent otolith Sr/Ca and Mn/Ca ratios signatures encompassing individuals among regions suggest that all local populations presents a high degree of dependence of estuarine system in

SW Atlantic Ocean, as recently suggested by Soeth et al. (2019a). Coastal and highly urbanized estuaries have experienced high rates of mangrove loss and habitat degradation (Osland et al., 2018) which may have potential ecological consequences for this species that showed a limited life cycle strategy in the first stages of life. The results also suggest that *C. faber* stock-recruitment projections may be largely derived from estuarine nursery areas, which should be monitored to calculate catch limits. However, the contribution that each local population receive from distant recruitment sources is unknown and demands further studies (Soeth et al., 2019b). The otoliths portions representing adult phase were more diverse regarding the elemental signatures and illustrate a more varied habitat use though this life stage. Inferential scope of seasonal movements was limited by environmental data lack (water chemistry) and unknown relative effects of environmental and physiological factors (Izzo et al., 2018; Sturrock et al., 2015). Further studies should be conducted to indicate whether environmental factors may outweigh physiological influences on otolith of the *C. faber*. Additionally, the application of high-resolution stable isotopic analysis will promote a better understanding of *C. faber* movements and estuarine use through all life stages.

Acknowledgments

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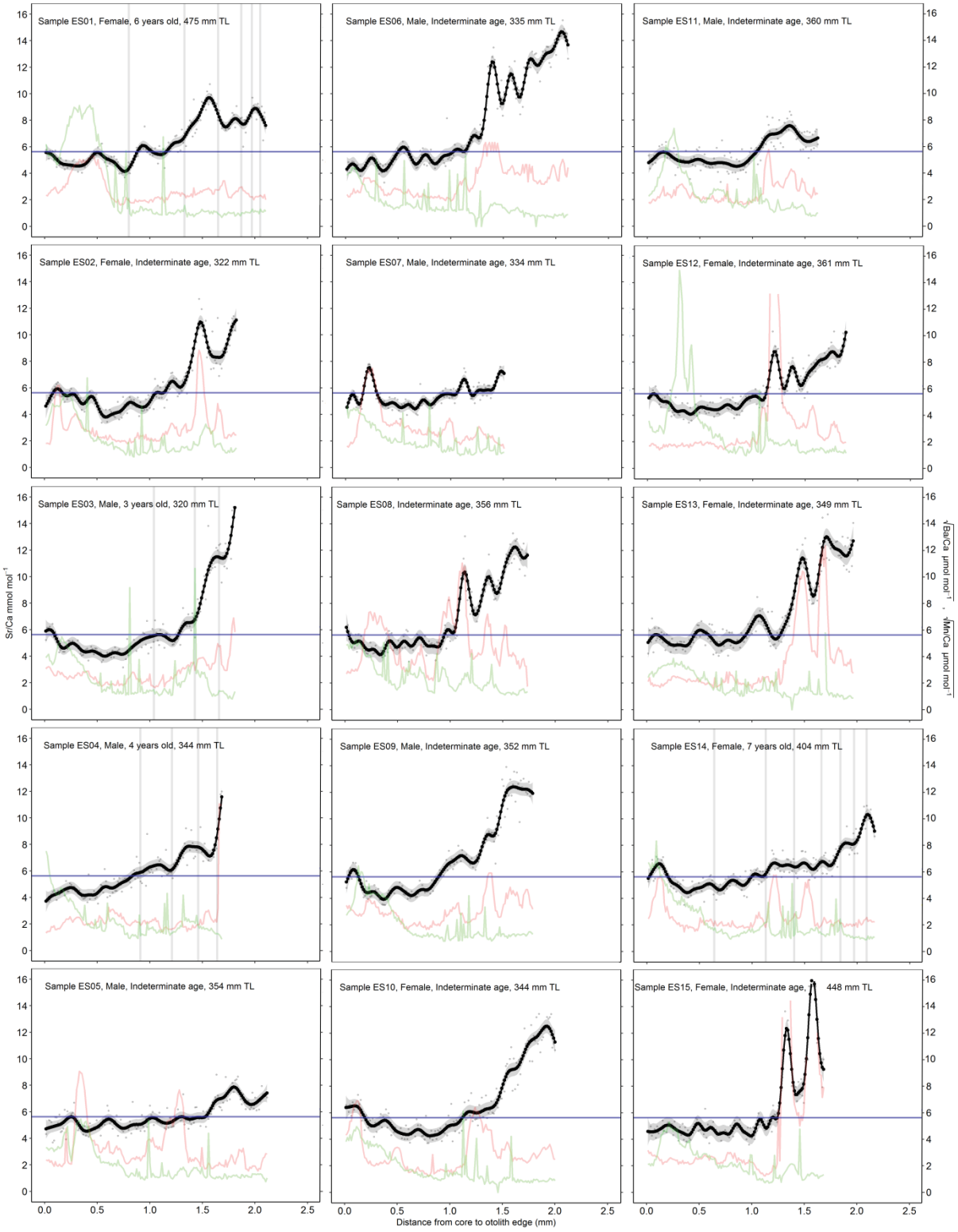
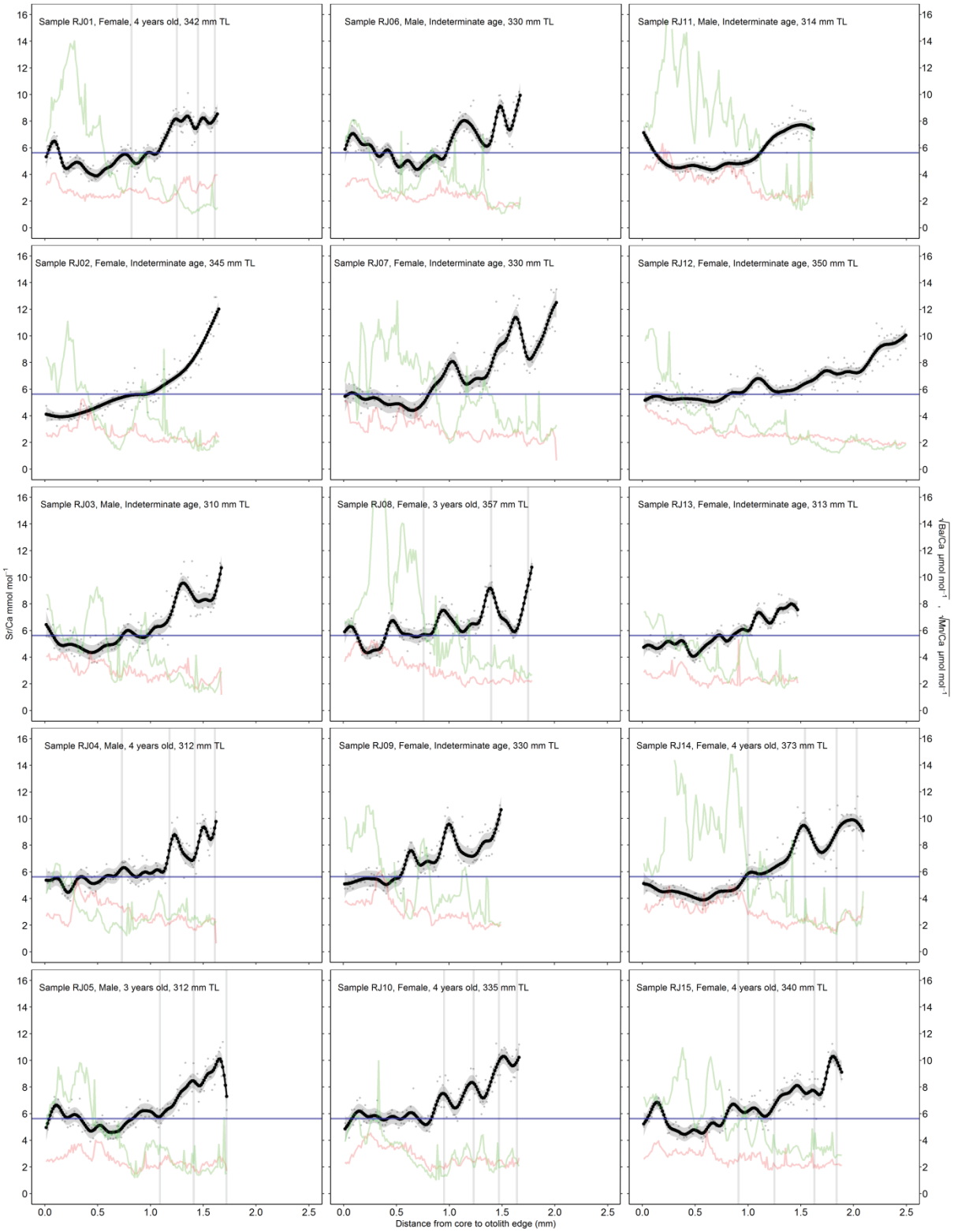
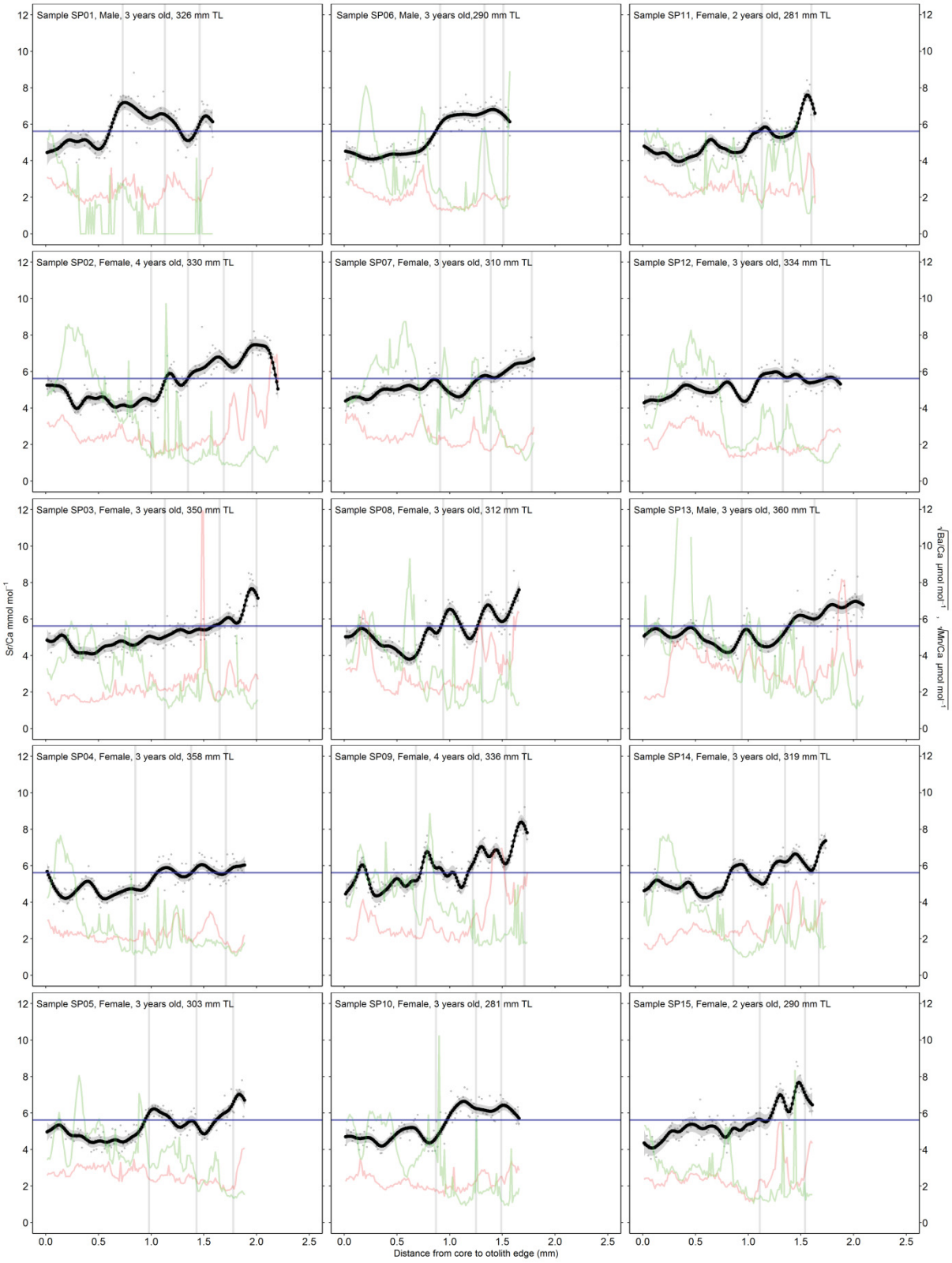
Supplemental files



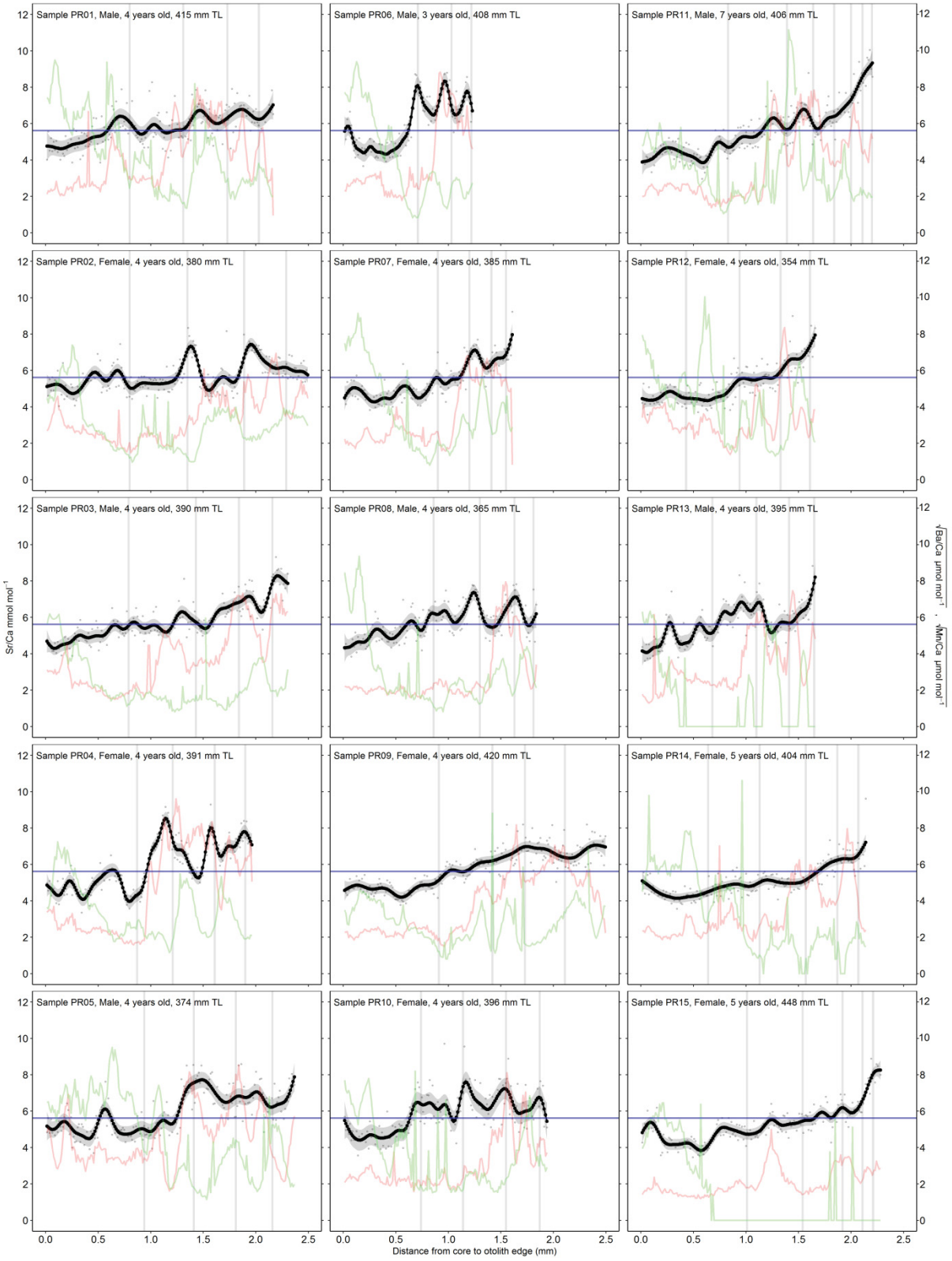
Supplementary file 1. Otolith microchemical profiles of *Chaetodipterus faber* from Espírito Santo (ES).



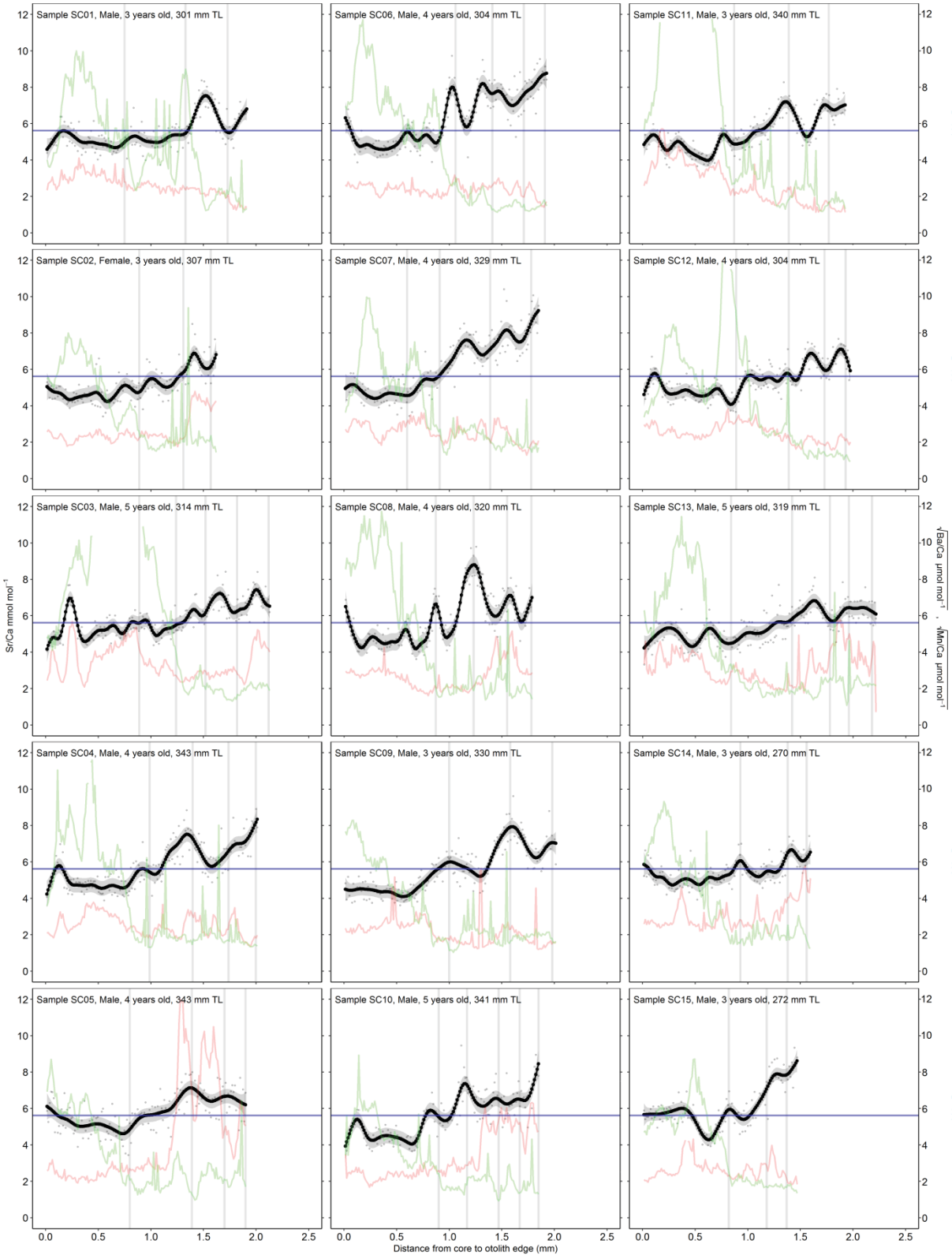
Supplementary file 2. Otolith microchemical profiles of *Chaetodipterus faber* from Rio de Janeiro (RJ).



Supplementary file 3. Otolith microchemical profiles of *Chaetodipterus faber* from São Paulo (SP).



Supplementary file 4. Otolith microchemical profiles of *Chaetodipterus faber* from Paraná (PR).



Supplementary file 5. Otolith microchemical profiles of *Chaetodipterus faber* from Santa Catarina (SC).

Supplementary table 1. Sample information: TL (total length, mm), Age (years). Generalized Additive Models (GAM) results for each individual fish analyzed and migratory pattern identified. Significant ($p < 0.001$) models are indicated by asterisk (*). Marine Migrant (MM) and Estuarine Visitor (EV). Region: Espírito Santo (ES); Rio de Janeiro (RJ); São Paulo (SP); Paraná (PR); Santa Catarina (SC).

Sample				GAM					Migratory
Region	Code	TL	Age	Mean	SE	edf	F	R^2-ajd	Pattern
	ES01	475	6	6.35	0.04	23.24	61.98*	0.92	MM
	ES02	322	Ind.	6.22	0.06	22.73	51.02*	0.92	MM
	ES03	320	3	6.27	0.06	19.87	95.31*	0.95	MM
	ES04	344	4	5.82	0.05	18.53	36.58*	0.88	MM
	ES05	354	Ind.	5.68	0.04	20.49	16.58*	0.74	MM
	ES06	335	Ind.	7.78	0.05	27.7	164*	0.97	MM
	ES07	334	Ind.	5.49	0.04	24.73	15.67*	0.83	EV
ES	ES08	356	Ind.	6.92	0.06	24.94	65.08*	0.94	MM
	ES09	352	Ind.	6.91	0.05	21.18	106*	0.96	MM
	ES10	344	Ind.	6.74	0.06	20.1	82.11*	0.94	MM
	ES11	360	Ind.	5.62	0.06	13.65	16.52*	0.72	MM
	ES12	361	Ind.	5.96	0.05	26.1	33.41*	0.89	MM
	ES13	349	Ind.	7.26	0.07	23.53	59.4*	0.93	EV
	ES14	385	7	6.24	0.04	24.79	37.65*	0.88	MM
	ES15	321	Ind.	6.25	0.06	28	82.56*	0.96	MM
	RJ01	342	4	5.94	0.05	22.11	31.41*	0.89	MM
	RJ02	345	Ind.	6.04	6.04	7.422	144.3*	0.92	MM
	RJ03	310	Ind.	6.35	0.07	16.79	29.56*	0.84	MM
	RJ04	312	4	6.33	0.06	22.55	17.66*	0.82	MM
	RJ05	332	3	6.44	0.06	22.21	24.1*	0.85	MM
RJ	RJ06	330	Ind.	6.36	0.06	21.58	17.91*	0.81	MM
	RJ07	330	Ind.	7.11	0.07	21.26	38.52*	0.88	MM
	RJ08	357	3	6.41	0.05	22.5	21.79*	0.83	MM
	RJ09	333	Ind.	6.85	0.07	18.13	17.94*	0.80	MM
	RJ10	335	4	6.90	0.07	18.21	24.7*	0.83	MM
	RJ11	314	Ind.	5.62	0.05	10.74	46.23*	0.84	MM

	RJ12	350	Ind.	6.58	0.04	18.97	42.54*	0.85	MM
	RJ13	313	Ind.	5.78	0.05	19.85	24.46*	0.86	MM
	RJ14	373	4	6.28	0.06	17.62	55.99*	0.89	MM
	RJ15	340	4	6.47	0.05	22.6	28.39*	0.86	MM
SP	SP01	326	3	5.77	0.05	13.97	14.15*	0.70	EV
	SP02	330	4	5.44	0.04	22.55	34.67*	0.86	EV
	SP03	350	3	5.17	0.04	21.12	18.13*	0.77	MM
	SP04	358	3	5.16	0.03	15.92	16.29*	0.71	EV
	SP05	303	3	5.26	0.03	20.43	18.81*	0.79	MM
	SP06	290	3	5.35	0.04	10.21	63.58*	0.88	MM
	SP07	310	3	5.30	0.04	15.06	15.34*	0.70	MM
	SP08	312	3	5.37	0.04	17.99	20.95*	0.81	EV
	SP09	336	4	5.82	0.04	24.62	23.04*	0.85	EV
	SP10	281	3	5.36	0.04	14.5	26.46*	0.81	MM
	SP11	298	2	5.06	0.04	19.05	26.86*	0.85	MM
	SP12	334	3	5.19	0.03	17.6	11.58*	0.67	EV
	SP13	360	3	5.46	0.04	17.75	17.98*	0.73	MM
	SP14	319	3	5.42	0.03	21.52	22.56*	0.84	EV
	SP15	292	2	5.47	0.05	20.97	15.06*	0.79	MM
PR	PR01	415	4	5.82	0.05	16.62	7.181*	0.50	EV
	PR02	380	4	5.73	0.04	23.88	11.04*	0.64	EV
	PR03	390	4	5.83	0.04	23.5	26.96*	0.82	EV
	PR04	391	4	5.89	0.04	26.1	45.09*	0.91	EV
	PR05	374	4	5.95	0.05	22.2	17.19*	0.73	MM
	PR06	428	3	5.97	0.06	19.63	23.34*	0.88	MM
	PR07	385	4	5.44	0.05	17.92	19.11*	0.80	MM
	PR08	365	4	5.72	0.05	20.77	9.722*	0.67	EV
	PR09	420	4	5.77	0.04	16.73	32.48*	0.79	MM
	PR10	396	4	5.87	0.06	22.02	8.096*	0.63	EV
	PR11	406	7	5.60	0.04	19.98	36.57*	0.85	EV
	PR12	354	4	5.28	0.05	12.75	21.94*	0.75	MM
	PR13	395	4	5.65	0.05	20.76	11.91*	0.74	EV
	PR14	404	5	5.08	0.04	13.68	24.42*	0.73	MM

	PR15	448	5	5.28	0.03	22.32	34.87*	0.85	MM
	SC01	301	3	5.50	0.04	15.36	15.53*	0.69	EV
	SC02	307	3	5.15	0.05	16.51	9.115*	0.64	MM
	SC03	314	4	5.81	0.04	27.75	15.27*	0.76	MM
	SC04	343	4	5.80	0.05	17.88	20.86*	0.77	MM
	SC05	345	4	5.80	0.06	12.43	11.24*	0.57	MM
	SC06	304	4	6.30	0.05	20.89	25.49*	0.83	MM
	SC07	329	4	6.18	0.06	15.55	33.01*	0.83	MM
SC	SC08	320	4	5.76	0.05	23.01	23.62*	0.85	EV
	SC09	330	3	5.59	0.05	15.45	34.18*	0.82	EV
	SC10	341	5	5.62	0.05	18.08	19.94*	0.78	MM
	SC11	340	3	5.51	0.04	19.72	23.96*	0.82	EV
	SC12	304	4	5.41	0.04	21.04	15.71*	0.75	MM
	SC13	319	5	5.46	0.05	17.54	11.86*	0.63	EV
	SC14	273	3	5.44	0.05	16.95	5.992*	0.55	MM
	SC15	272	3	6.05	0.05	12.65	30.92*	0.83	MM

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CAPÍTULO 5

Considerações finais

CONSIDERAÇÕES FINAIS

Na presente tese foram analisados importantes aspectos biológicos, ecológicos e espaço-temporais de *Chaetodipterus faber* no Oceano Atlântico Sudoeste. A integração de diferentes abordagens teve o objetivo final de conhecer a história de vida e a estrutura populacional da espécie nesta região. O conjunto de informações aqui apresentado pode ser implementado em diferentes modelos de manejo pesqueiro, incluindo os métodos tradicionais no qual ações de manejo são tomadas em nível de espécie e populações, assim como em ações de manejo realizado em nível ecossistêmico, o qual apresenta uma crescente demanda sobre o entendimento dos processos ecológicos e espaciais de populações e espécies (Lowerre-Barbieri et al., 2019; Patrick and Link, 2015; Secor, 2013).

Próximo ao seu limite sul de distribuição os otólitos sagittae de *C. faber* apresentaram ciclos anuais de incrementos de crescimento adequados para estimativa de idade dos indivíduos. Nesta região o crescimento corpóreo anual do paru é moderado e uma longevidade de 17 anos foi encontrada. Embora a fecundidade da espécie não tenha sido estimada na presente tese, o paru matura precocemente (< 2 anos), apresenta índices gonodossomáticos elevados e realiza desovas parceladas durante um período reprodutivo prolongado (> 3 meses). Na região do Paraná, os indivíduos capturados pela pesca artesanal apresentaram idades entre dois e 17 anos. A maturação precoce de *C. faber* nesta região permite que grande parte dos indivíduos se reproduza ao menos uma vez antes de atingir o tamanho comercial. Adicionalmente, a espécie forma agregados estuarino-costeiros com propósitos reprodutivos durante a primavera e verão (outubro a janeiro) no Paraná. O comportamento reprodutivo encontrado provavelmente aumenta as chances do recrutamento pós-larval de *C. faber* ocorrer em áreas favoráveis ao seu desenvolvimento. Entretanto, a alta densidade de indivíduos adultos em locais e períodos previsíveis facilita a captura dos indivíduos e aumenta o risco de sobrexplotação pesqueira (De Mitcheson et al., 2008; van Overzee and Rijnsdorp, 2014). De fato, os maiores desembarques de paru pela frota artesanal coincidem com o período de maior atividade reprodutiva identificado para a espécie (PMAP-BS 2017a, 2017b). Os resultados fenotípicos apresentados no terceiro capítulo indicaram que o estoque explotado nesta latitude poderia ser gerido localmente, o que provavelmente facilitaria o delineamento de um processo de manejo participativo do recurso. Contudo, os padrões migratórios verificados ao longo dos marcos cronológicos dos otólitos no capítulo 4 evidenciaram que uma parcela dos indivíduos realiza movimentações regulares para regiões de maiores salinidades, provavelmente para áreas mais distantes da costa. Neste sentido, o

estoque explotado pela frota artesanal estuarino-costeira durante a primavera e verão pode ser acessível à frota industrial de cerco em outras áreas, principalmente no inverno, período no qual a frota industrial desembarca as maiores biomassas da espécie (UNIVALI/CTTMar, 2010, 2013a, 2013b; PMAP-BS, 2017a, 2017b; PMAP-SC, 2018). Desta forma, considerando as grandes escalas espaciais que a frota industrial opera, ações de governança devem ser tomadas em maiores escalas regionais, uma vez que a pesca realizada em diferentes isóbatas e por diferentes modalidades pesqueiras podem estar incidindo sobre o mesmo estoque (Cooke et al., 2011). Considerando o elevado potencial de captura da frota industrial de cerco e os múltiplos usuários deste recurso, é evidente que medidas precautórias de manejo pesqueiro sejam implementadas imediatamente para priorizar a resiliência das populações da espécie e a segurança alimentar das comunidades tradicionais costeiras (Abreu-Mota et al., 2018; Pauly et al., 2005). Atualmente não há medida de manejo que restrinja as capturas de paru, excetuando-se as áreas de exclusão de pesca por modalidade de petrecho e as pequenas unidades de conservação ao longo da costa brasileira. O estabelecimento de períodos de defeso e áreas de exclusão de pesca são medidas eficientes de manejo para espécies que formam grandes agregados reprodutivos e devem ser consideradas em ações futuras (van Overzee and Rijnsdorp, 2014).

Durante seu ciclo de vida, *C. faber* utiliza uma ampla variedade de habitats e se depara com diferentes pressões ambientais e antropogênicas, diretas e indiretas, as quais devem ser contabilizadas no manejo deste recurso. *Chaetodipterus faber* faz parte da fauna acompanhante previsível, especialmente nas modalidades de arrasto onde exemplares da espécie com tamanho médio de 25 cm de comprimento total são predominantes nos desembarques (PMAP-SC, 2018; Rotundo et al., 2019). Durante as migrações entre áreas estuarinas e recifais costeiras os indivíduos da espécie atravessam extensas matrizes arenosas e ficam suscetíveis a frota de arrasto e outras frotas multiespecíficas. Neste sentido, o tamanho mínimo de captura (25 cm CT) deve ser estabelecido para proibir a captura e comercialização de indivíduos imaturos. Além disso, para a pesca de arrasto, o uso de redutores de fauna acompanhante em conjunto com modificações nos ensacadores das redes de arrasto (ex., abertura de escape superior) pode ter uma eficiência de exclusão de até 77% dos indivíduos desta espécie (Steele et al., 2002). Estas modificações podem ser empregadas para reduzir do impacto da pesca de arrasto e favorecer a conectividade demográfica da espécie.

Em nível de estrutura populacional a abordagem química e de forma dos otólitos apresentou resultados bastante satisfatórios e que podem ser incorporadas em medidas futuras

de manejo pesqueiro da espécie. O uso combinado da forma e da química dos otólitos maximizou a classificação dos indivíduos em sua região de origem e corroborou com a estrutura genética conhecida em nível de DNA mitocondrial entre a região tropical e subtropical do Brasil (Machado et al., 2017). Considerando a dinâmica populacional, avaliações adicionais com um maior número de amostras e replicação temporal devem ser realizadas para confirmar a estrutura espacial identificada. Além disso, a obtenção de amostras da frota industrial e de outras localidades promoverá um maior entendimento da estruturação do estoque pesqueiro.

No que diz respeito aos padrões migratórios, os registros químicos nas porções dos otólitos representando a fase juvenil de vida sustentaram que a espécie utiliza de forma majoritária os estuários nesta fase do seu ciclo de vida. Há que se destacar que, outros possíveis padrões migratórios, provavelmente menos frequentes nas populações de *C. faber*, como por exemplo, estuarino residente e marinho residente podem ocorrer, mas não foram presentes nas 75 amostras analisadas (Secor, 1999). Contudo, os resultados obtidos reforçam a importância da conservação dos ambientes estuarinos que contribuem expressivamente para a manutenção das populações de *C. faber* no Oceano Atlântico Sudoeste. Os ambientes estuarinos têm experienciado um aumento de degradação ocasionado principalmente pela expansão urbana e portuária as quais tem suprimido áreas de manguezais, intensificado as operações de dragagens e a liberação de efluentes domésticos e industriais nestas regiões (Barletta et al., 2010; Osland et al., 2018; Valiela et al., 2001). Não há dados no momento para estimar precisamente as consequências ecológicas sobre a espécie em questão, mas os efeitos deletérios devem ser evitados por meio da conservação destas áreas e um planejamento espacial costeiro que mantenha a funcionalidade e os *trade-offs* dos serviços ecossistêmicos (Gillanders et al., 2012; Laegdsgaard and Johnson, 2001; Mumby and Hastings, 2008).

Na presente tese, significativos avanços no entendimento da ecologia da espécie foram alcançados, porém, várias questões ecológicas permanecem abertas e algumas recomendações podem ser elencadas para o preenchimento destas lacunas. Primeiramente, existe a necessidade de se avaliar qual a contribuição das áreas berçários para cada estoque explotado comercialmente (Correia et al., 2014; Reis-Santos et al., 2013b). No que se refere à reprodução, estimativas de fecundidade dependente da idade e do tamanho dos indivíduos são ainda necessárias para mensurar o potencial reprodutivo dos estoques (Cooper et al., 2013; Hixon et al., 2014). O período reprodutivo e a idade dos indivíduos foram determinados por uma amostragem robusta, todavia, considerando a ampla distribuição da espécie e da estrutura do estoque identificado, avaliações em maiores escalas espaciais são necessárias. Para *C.*

faber, o índice gonodossomático foi diretamente relacionado com o período reprodutivo e pode ser utilizado para dar suporte a definição deste em locais onde restrições logísticas existem (Fontoura et al., 2018).

Embora tentativas tenham sido realizadas, as amostras provenientes das pescarias direcionadas à *C. faber* foram insuficientes para se calcular as taxas de explotação pesqueira. Para isso, é recomendado um monitoramento continuo e abrangente das diferentes pescarias que incidem sobre os estoques deste recurso. Informações sobre as classes etárias pescadas pelas diferentes modalidades pesqueiras são necessárias para o cálculo dos níveis de explotação, monitoramento da estrutura etária dos estoques pesqueiros e definição dos limites anuais de captura (Aschenbrenner et al., 2017; Clark, 1991).

A química de otólito é uma ciência em desenvolvimento e embora muito avanço tenha ocorrido nas últimas duas décadas, a execução de muitos métodos analíticos da temática é dependente de equipamentos sofisticados, com elevado custo de utilização e acesso limitado (Secor, 2010; Tanner et al., 2015; Walther, 2019). Na presente tese, uma análise adicional e de alta resolução temporal dos isótopos de $\delta^{18}O$ (indicador para temperatura), $\delta^{13}C$ (indicador para influência terrestre) e $\delta^{15}N$ (indicação trófica) nas amostras dos otólitos poderia ter auxiliado na interpretação dos padrões migratórios (Darnaude and Hunter, 2018; Sturrock et al., 2015). Além disso, frente às possibilidades de controle fisiológico na incorporação de alguns elementos químicos, a obtenção de amostras de parus jovens e adultos em diferentes ambientes e profundidades e/ou experimentos laboratoriais são necessários para avaliar o efeito interativo da ontogenia, reprodução, temperatura e salinidade na incorporação de diferentes elementos químicos (Izzo et al., 2018; Sturrock et al., 2015). O efeito de variáveis ambientais (ex., salinidade e temperatura) sobre a densidade e distribuição da espécie por meio da modelagem ecológica (GLM) com dados históricos disponíveis também é exequível e pode corroborar os movimentos ontogenéticos evidenciados pelas assinaturas químicas dos otólitos analisados. E por fim, uma caracterização geoquímica das massas da água na plataforma continental do Sudeste e do Sul do Brasil permitiria uma interpretação refinada das assinaturas químicas nos otólitos e a definição de fronteiras ecológicas para esta e outras espécies da região.

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